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NEW STEROID COMPOUNDS WITH PROGESTATIONAL ACTIVITY *

Consulting Editor

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INTRODUCTORY REMARKS

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When steroid hormones were first being isolated and characterized some investigators impressed with the remarkable actions of these substances were inclined to regard them as possessed of the highest order of activity upon which man could not further improve However the ingenuity of the synthetic chemist working in concert with the endocrinologist has convincingly refuted this attitude Thus we have seen the advent of an era marked with striking success in the synthesis of steroidal derivatives not only more potent in some respects than the naturally occurring compounds but skillfully devised to retain the favorable actions desired with a minimum of contraindicatory effects

These substances have included the anabolic steroids with potent nitrogen retaining myotrophic activity and lesser androgenic qualities and the Δ^1 derivatives of the 11 oxysteroids which exert more potent beneficial actions on inflammatory states in man with a dampening of the undesirable effects on water and electrolyte metabolism

In this monograph another manifestation of this trend is considered—the newly synthesized steroids with progestational activity We look forward with interest to the unfolding of information concerning their nature biological activities and their increasing applications to clinical states in man

INTRODUCTION

By Abraham E Rakoff
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It is of interest to recall that evidence for the existence of a corpus luteum hormone dates back more than 50 years In 1903 Frankel[1] showed that the removal of the corpora lutea of rabbits in the first few days of pregnancy invariably caused the embryos to disappear and in 1907 Loeb[2] discovered that the corpus luteum specifically alters the uterus of the guinea pig so that implantation becomes possible In 1910 Bouin and Ancel[3] described the progestational proliferation in the endometrium of the rabbit under the influence of corpora lutea It was not until 1929[4] however that the hormone of the corpus luteum responsible for the progestational proliferation was shown by Corner and Allen to be present in lipoid extracts of the corpus luteum Potent crystalline preparations were prepared in 1931 by Fels and Slotta[5] and in 1932 by Allen[6] and by Fevold and Hisaw[7]

The isolation of pure progesterone was announced almost simultaneously in 1934 by a number of workers including Butenandt[8] Slotta Ruschig and Fels[9] Allen and Wintersteiner[10] and Hartmann and Wettstein[11]

The synthesis from stigmasterol and from pregnandiol and the establishment of the structural formula of progesterone was also achieved in that year

Although much was expected from the therapeutic use of progesterone in various gynecologic and obstetric dysfunctions the small amount available and the expense of the preparation delayed the recognition of the true value of this hormone in those conditions until the availability of higher dosage preparations The gynecologist now recognizes progesterone as the therapeutic agent of choice in the treatment of many ovarian and menstrual disorders and most obstetricians give progesterone with or without estrogen as part of their routine therapy in the management of threatened abortion or in the prophylaxis of habitual abortion although the Council on Pharmacy and Chemistry of the American Medical Association Chicago Ill maintains that there is insufficient satisfactory evidence to establish its effectiveness for these conditions

It has been recognized also that progesterone has certain practical limitations as a therapeutic agent among which may be listed its relative ineffectiveness by the oral route its limited solubility in oily vehicles and its tendency to give painful local reactions on injection of crystalline suspensions or sometimes with larger doses in oily solution Preparations of progesterone for buccal or vaginal absorption were introduced to avoid frequent intramuscular injection although the relative potency by these routes was diminished and administration by these routes often was not convenient

The introduction of anhydrohydroxyprogesterone or ethisterone provided the first compound for therapeutic use that exerted a considerable progesteronelike action when given orally as shown by Inhoffen and Hohlweg[12] in

1938 and Courrier and Jost[13] in 1939. Although its potency was only one fifth to one tenth that of progesterone given by injection as demonstrated by Miescher and Gasche[14] in 1943 and by Greenblatt[15] in 1944 it represented an important advance in convenience of administration

In the last several years there has been a remarkable renewal of interest in compounds with progesterone activity in the discovery of new preparations with high progestational activity These however have excited much interest not only because they possess properties that represent therapeutic advantages such as prolonged duration or high oral potency but also because they possess properties that differ from progesterone and from each other in their biologic actions in man and in various animal species and also in their metabolism and excretion products

Many investigators in the United States and elsewhere both in the laboratory and in the clinic are currently devoting much time and effort to the study of these new progestational agents This monograph was proposed because of the obvious need for the first hand exchange of information on the various aspects and problems involved in these new developments

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SOME BIOLOGICAL ACTIVITIES OF CERTAIN PROGESTOGENS I 17α HYDROXYPROGESTERONE 17 n CAPROATE

By Woodrow B Kessler and Aleck Borman
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17α Hydroxyprogesterone caproate (HPC)* has been found to be an active progestational agent possessing a markedly prolonged duration of action [1, 2] The low order of activity of unesterified 17α hydroxyprogesterone (HP)[3] makes the biological efficacy of HPC all the more unusual Although increases in potency are noted upon esterification of certain androgenic and estrogenic steroids the magnification of potency following esterification of HP is uniquely high

The qualitative and quantitative differences in biological effects noted following alteration in steroidal structure[4] made it of interest to examine a spectrum of endocrine responses Thus in addition to the progestational activity of HPC androgenic glucocorticoid mineralocorticoid and anti uterotrophic properties were assessed

Progestational Studies

Immature virgin female Flemish rabbits were injected for 6 days with 5 μg of estradiol in 0 5 ml of sesame oil and then treated with 4 daily doses of progesterone HPC or HP During the 4 day treatment period the daily estrogen dosage was lowered to 0 5 μg Segments of uteri were taken on the fifth day for histological evaluation by the method of McPhail [5] A summary of the results is recorded in TABLE 1 and the structure activity relationships are presented in FIGURE 1 The decrease in progestational efficacy of progesterone following 17α hydroxylation is completely reversed by subsequent esterification with caproic acid and this also leads to a potentiation of progesterone

Administration of single subcutaneous doses of HPC in an ethyl lactate castor oil vehicle to rabbits subsequently autopsied at various intervals confirmed Junkmann s report[1] that this material possessed a depot action (FIGURE 2) The delay in onset of activity as compared with progesterone (FIGURE 2) was overcome by changing the vehicle to benzyl benzoate sesame oil (FIGURE 3) The earlier peak response noted had no discernible effect on the duration of activity which was seen to persist for nearly three weeks

Androgenic and Glucocorticoid Studies

Doses of HP HPC, and testosterone were administered daily for twenty days by the subcutaneous route to immature castrated male rats The animals were autopsied on the twenty first day and organ weights were

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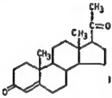
TABLE 1
EFFECTS OF MODIFICATION OF PROGESTERONE ON BIOLOGICAL POTENCY IN FEMALE RABBITS

Compound	Number of rabbits	Total dose (mg)	Degree of progestational proliferation
Progesterone	8	1 0	+4 +4 +2 +4 +3 +4 +4 +4
	6	0 5	+2 +2 +3 +2 +2 +1
	6	0 25	+2 +1 0 +1 +1 +1
17α hydroxy progesterone	4	50 0	+2 0 +2 +1
	4	25 0	0 0 0 0
17α hydroxyprogesterone caproate	6	1 0	+3 +4 +4 +4 +4 +3
	6	0 5	+4 +4 +3 +4 +1 +3
	4	0 25	+3 +2 +3 +2
	5	0 125	+1 +1 +2 0 +1
	4	0 06	0 +1 0 0

By the method of McPhail[5]



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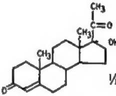
PROGESTERONE



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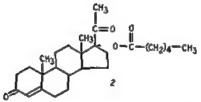
17α HYDROXYPROGESTERONE



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17α HYDROXYPROGESTERONE 17 n CAPROATE

FIGURE 1 *Progestational activities of structurally* modified progesterones in rabbits

recorded (TABLE 2) Although the higher doses of testosterone proved thymolytic neither HP nor HPC showed such activity In contrast administration of both HP and HPC tended to increase adrenal weights A well defined prostatic hypertrophy was evident following administration of HP but no androgenic activity was noted with comparable doses of HPC (TABLE 2)

The lack of glucocorticoid activity indicated by the absence of thymolysis following administration of HP or HPC is borne out in liver glycogen studies carried out by the method of Pabst *et al* (TABLE 3)[6] Thus HP and HPC have little or no glucocorticoid activity

Mineralocorticoid Studies

Measurements of urinary sodium excretion were made in intact and adrenalectomized male rats by a modification of Dorfman's procedure[7] In brief, the method consisted of administering a sodium load containing

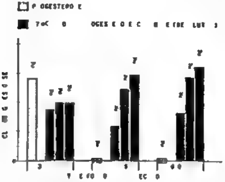

FIGURE 2 Comparative effect of a single subcutaneous injection of HPC and progesterone in ethyl lactate–castor oil on progestational changes in the rabbit uterus The values are averages for 4 animals

Na[22] collecting urine for 5 hours and then measuring the labeled sodium excreted during this period Some adrenalectomized rats were given subcutaneous injections of steroidal material 1 hour prior to the administration of the sodium load on the fourth day following surgery In another group of adrenalectomized animals steroid administration was begun on the day

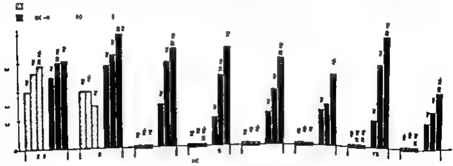

FIGURE 3 Comparative effect of a single subcutaneous injection of HPC and progesterone in benzyl benzoate–sesame oil on progestational changes in the rabbit uterus The values are averages for 4 animals

of adrenalectomy and carried on for 2 subsequent days on the fourth day following adrenalectomy these animals received only the sodium load containing Na[22] Both types of studies were also carried out in intact rats The heightened sodium excretion of adrenalectomized rats after a sodium load was approximated in intact male rats pretreated with HPC for 3 days (TABLE 4) Moreover animals treated with 0 3 mg of progesterone daily

TABLE 2

EFFECT OF 17α HYDROXYPROGESTERONE AND 17α HYDROXYPROGESTERONE CAPROATE ON ORGAN WEIGHTS

Daily treatment for 20 days	No rats	Initial body wgt (gm)	Body wgt autopsy twentieth day (gm)	Seminal vesicles wet wgt (mg)	Ventral prostate wet wgt (mg)	Thymus wgt (mg)	Adrenals (mg)	Adrenals (mg/100 gm body wgt)
0.5 cc Sesame oil	10	60	203	18.12 ± 2.17*	12.57 ± 1.70*	763.3 ± 27.3	35.23 ± 4.56	17.51 ± 2.73*
1 mg 17α hydroxyprogesterone caproate	10	61	208	20.32 ± 1.03	11.12 ± 1.40	795.1 ± 48.95	47.50 ± 6.48	22.84 ± 2.98
5 mg 17α hydroxyprogesterone caproate	10	60	198	17.56 ± 1.33	8.48 ± 0.97	821.0 ± 62.68	47.00 ± 2.86	23.74 ± 1.08
10 mg 17α hydroxyprogesterone caproate	10	60	208	17.10 ± 1.27	9.90 ± 0.77	768.8 ± 34.60	48.30 ± 1.90	23.40 ± 1.62
1 mg 17α hydroxyprogesterone	11	59	186	16.46 ± 1.75	19.55 ± 0.92	814.8 ± 37.49	49.5 ± 1.54	27.72 ± 3.78
5 mg 17α hydroxyprogesterone	10	60	199	27.40 ± 4.31	25.08 ± 2.67	659.4 ± 25.38	45.46 ± 2.26	22.88 ± 0.46
10 mg 17α hydroxyprogesterone	10	62	210	18.35 ± 2.24	26.24 ± 3.95	813.0 ± 94.98	38.1 ± 3.71	18.09 ± 1.23
100 μg Testosterone	10	59	206	89.2 ± 4.04	50.9 ± 2.50	660.2 ± 25.19	37.39 ± 2.69	18.29 ± 1.74
500 μg Testosterone	10	59	210	194.2 ± 17.73	169.5 ± 10.11	538.3 ± 59.83	34.59 ± 2.29	16.47 ± 0.61
1 mg Testosterone	10	63	204	264.9 ± 33.57	191.4 ± 14.80	497.2 ± 45.95	35.29 ± 1.25	17.32 ± 0.42

* Standard deviation of the mean

TABLE 3
LIVER GLYCOGEN DEPOSITION IN RATS FOLLOWING ADMINISTRATION OF 17α HYDROXYPROGESTERONE AND 17α HYDROXYPROGESTERONE CAPROATE

Compound	Number of rats	Dose (μg)	Per cent glycogen
Twenty five per cent Tween	10	—	0.09
E Acetate	4	200	0.45
	4	280	0.52
	4	400	1.10
	4	560	1.34
17α Hydroxyprogesterone caproate	4	400	0.12
	4	560	0.11
	4	800	0.09
	4	1120	0.08
	4	1600	0.11
17α Hydroxyprogesterone	4	400	0.11
	4	560	0.08
	4	800	0.08
	4	1120	0.12
	4	1600	0.10

The vehicle used for all groups was 25 per cent Tween 80

TABLE 4
EFFECT OF PRETREATMENT WITH 17α HYDROXYPROGESTERONE CAPROATE ON THE SODIUM EXCRETION OF INTACT MALE RATS

Treatment	Number of rats	Do	Na^{22} excretion in 5 hours after sodium load (cpm)	Range
Adrenalectomy	5		17 684	12 073–20 031
Intact	5		10 469	3 014–19 710
Intact + 17α hydroxyprogesterone caproate (3 days)	5	0.5 mg/day	14 536	12 224–17 856
Intact + 17α hydroxyprogesterone caproate (3 days)	5	2.0 mg/day	11 341	7 112–15 277
Intact + 17α hydroxyprogesterone caproate (3 days)	5	4.0 mg/day	18 001	11 140–23

Body weight of rats 200 to 250 gm input 290 250 cpm/rat/0.5 ml carrier 0.1 mg NaCl/gm body weight

TABLE 5

EFFECT OF PRETREATMENT WITH PROGESTERONE AND 17α HYDROXYPROGESTERONE CAPROATE ON SODIUM EXCRETION OF INTACT MALE RATS

Treatment	Number of rats	Dose	Na excretion in 5 hours after sodium load (cpm)	Range
Intact untreated	5	—	9 102	3 876–12 149
Intact sesame oil (3 days)	5	0 25 ml /day	10 382	6 835–14 938
Intact 17α hydroxyprogesterone caproate (3 days)	5	0 3 mg /day	11 066	4 886–15 979
Intact 17α hydroxyprogesterone caproate (3 days)	5	1 6 mg /day	10 643	2 157–18 319
Intact 17α hydroxyprogesterone caproate (3 days)	4	8 3 mg /day	18 167	16 384–19 322
Intact progesterone (3 days)	5	[illegible] 3 mg /day	22 783	14 689–30 162
Intact progesterone (3 days)	5	1 6 mg /day	19 132	5 075–33 029
Intact progesterone (3 days)	5	8 3 mg /day	10 432	4 614–14 461
Adrenalectomized untreated	5		19 110	15 493–24 276

Body weight of rats 225 to 250 gm input 307 650 cpm/rat/0 5 ml carrier 0 1 mg NaCl/gm body weight

TABLE 6

EFFECT OF PROGESTERONE PRETREATMENT ON THE URINARY EXCRETION OF SODIUM IN ADRENALECTOMIZED MALE RATS FOLLOWING ADMINISTRATION OF 9α CHLOROHYDROCORTISONE ACETATE

Treatment	Number of rats	Dose	Na^{22} excretion 5 hours after sodium load (cpm)	Range
—	4	—	17 800	15 700–22 600
9α Chloro F acetate	4	0 5 μg	5 300	1 760–11 900
9α Chloro F acetate	4	2 5 μg	3 290	1 540– 5 450
Progesterone (3 days)	4	300 μg /day	12 000	10 000–16 400
Progesterone (3 days) 9α Chloro F acetate	4	300 μg /day 0 5 μg	11 500	5 000–17 500
Progesterone (3 days) 9α Chloro F acetate	4	300 μg /day 2 5 μg	8 590	6 900–15 700
Progesterone (1 hr prior)	4	1 0 mg	10 800	8 100–14 300
Progesterone (1 hr prior) 9α Chloro F acetate	4	1 0 mg 0 5 μg	11 600	9 330–13 900
Progesterone (1 hr prior) 9α Chloro F acetate	4	1 0 mg 2 5 μg	3 110	1 660– 5 670

Body weight of rats 120 to 150 gm input 386 470 cpm/rat/0 5 ml carrier 0 1 mg NaCl/gm body weight

for 3 days excreted more sodium than rats given comparable doses of HPC Indeed 8 3 mg of HPC per day for 3 days was required to obtain the level of sodium excretion seen with 0 3 mg of progesterone (TABLE 5)

Pretreatment with progesterone for 3 days or administration 1 hour prior to the sodium load resulted in sodium retention in adrenalectomized rats In spite of this effect pretreatment with progesterone was capable of partially reversing a sodium retention due to administration of 9α chlorohydrocortisone acetate (TABLE 6) It is noteworthy that no reversal of 2 5 μg of 9α chlorohydrocortisone acetate was observed in animals treated acutely with progesterone The activities of HP and HPC as anti sodium retaining agents are under investigation in adrenalectomized rats

Anti Estrogen Studies

A substantial reduction in progestational potency in rabbits is noted following the introduction of 9α halogen and 11β hydroxyl groups into progesterone[8] However Huggins[9] has shown that 9α fluoro 11β hydroxyprogesterone (FHP) is considerably more active than progesterone as an estrogen antagonist It was of interest to determine the effects of 17α hydroxylation and esterification on the anti estrogenic activity of progesterone

Combinations of estradiol with progesterone FHP HP or HPC were administered to immature female mice as 3 daily intramuscular doses in

TABLE 7

COMPARISON OF ANTI ESTROGENIC ACTIVITIES OF SOME PROGESTAGENS

Compound	Total dose	Avg body weight* (gm)	Uterine weight (mg)		Per cent inhibition	
			Wet	Dry	Wet	Dry
Sesame oil	—	10 8	9 2	1 9	—	—
Estradiol	0 015 μg	10 6	25 3	4 3	—	—
Estradiol	0 03 μg	12 5	39 4	5 8	—	—
Estradiol	0 06 μg	11 7	48 6	6 8	—	—
FHP + 0 03 μg estradiol	10 0 μg	11 9	24 8	4 3	46	37
	5 0 μg	12 1	27 7	4 6	37	28
	2 5 μg	12 3	31 5	5 1	24	17
17α hydroxyprogesterone caproate + 0 03 μg estradiol	160 μg	10 5	38 3	5 9	−21	−32
	40 μg	10 3	38 9	6 3	−26	−49
	10 μg	13 0	41 9	6 7	−3	−16
17α hydroxyprogesterone + 0 03 μg estradiol	160 μg	12 7	34 1	5 6	20	7
	40 μg	12 9	39 1	6 2	5	−4
	10 μg	11 2	40 8	6 4	−21	−35
Progesterone + 0 03 μg estradiol	50 μg	12 3	21 1	3 8	63	55
	10 μg	13 7	32 9	5 6	33	21

* Ten mice per group

$$\text{Percentage of inhibition} = 100 - \left[\frac{\text{experimental} - \text{control}}{0\ 03\ \mu g\ \text{estradiol} - \text{control}} \times 100\right]$$

0 1 ml sesame oil with autopsy on the fourth day The uterotrophic responses of mice to estrogenic materials have been described by Rubin *et al* [10] and the inhibition of this response has served as our end point of anti estrogenic activity FHP proved a more potent antagonist of estradiol in the mouse than did progesterone in confirmation of Huggins rat data [9] Moreover neither HP nor HPC showed much activity as anti uterotrophic agents Indeed HPC was slightly stimulatory in these studies (TABLE 7) Thus both anti uterotrophic and progestational activities are virtually abolished when progesterone is hydroxylated in the 17α position While progestational activity in the rabbit returns with subsequent esterification anti uterotrophic activity in the mouse remains absent from this modified progestagen

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SOME BIOLOGICAL ACTIVITIES OF CERTAIN PROGESTOGENS II. 9- AND 12-HALO-11-OXYGENATED PROGESTERONES

By Josef Fried, Woodrow W. Kessler, and Aleck Borman
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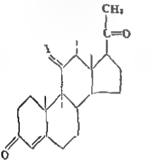
Enhancement of biological activity by 9α-halogenation of the cortical hormones was the subject of a paper published in a monograph of The New York Academy of Sciences less than two years ago.[1] The emphasis at that time was on the adrenocorticoid properties of the 9α-halogenated derivatives of the more highly hydroxylated hormones, particularly hydrocortisone. It was shown that maximum activity was exhibited by the fluorinated compounds and that there was a progressive decrease in potency when the heavier halogens were substituted for fluorine. The high degree of potentiation achieved by this structural modification made it possible for the first time to replace the hydroxylated side chains of hydrocortisone and of corticosterone—believed to be essential for corticoid activity—by the simple acetyl side chain of progesterone and still retain appreciable corticoid activity. More recent biological studies of the resulting 9α-halo-11-oxygenated progesterones and of their 12α-halogenated analogues[2] outside of the corticoid area have resulted in the discovery of their anti-uterotrophic and progestational properties, which form the subject of this paper.

TABLE 1 represents a more complete record than was available in 1955[1] of the activities of the 9α- and 12α-halo-11β-hydroxy and 11-ketoprogesterones in the rat liver glycogen[4] and sodium retention assays.[5] These data clearly show the gradual increase in glycogenic activity with decreasing atomic weight of the halogen atom. In the case of the sodium retention assay only the fluorinated derivatives show pronounced activity, the activity of the remaining members of the series being negligible. The remarkable almost quantitative parallelism of the activities of the 9α- and 12α-halo derivatives[2] has served to support the hypothesis that the activity-enhancing properties of the halogen atom are a function of the latter's electronegativity, that is, of the varying facility of the individual halogens in withdrawing electrons from the neighboring 11β-hydroxyl group and thereby increasing the acidic character of the latter.[6] Such a hypothesis is especially attractive since it visualizes a transfer of the effect of the halogen onto the 11β-hydroxyl group, which is considered vital for corticoid activity. It may be concluded from the above considerations that structure-potency relationships of the type hitherto discussed should apply only to those activities for which the presence of the 11β-hydroxyl group is essential. As we shall see later, the effects of the various halogens on progestational and anti-uterotrophic activity are of quite a different nature.

Huggins and Jensen[7] were the first to show that 9α-halogenation of 11-oxygenated steroids could enhance potency outside of the corticoid area. These workers, while studying the influence of chemical structure on the anti-uterotrophic activity of various steroids, found that in contrast to

progesterone which was a potent inhibitor of the uterotrophic activity of estrone in the hypophysectomized rat 11β hydroxyprogesterone possessed considerably lower activity On the other hand 11β hydroxyprogesterone was more potent than progesterone in inhibiting the uterotrophic activity of testosterone in the hypophysectomized rat (TABLE 2) 9α Fluoro 11β hydroxyprogesterone was found to be considerably more potent than 11β hydroxyprogesterone in antagonizing the uterotrophic effects of both estrone

TABLE 1
ADRENOCORTICOID ACTIVITY OF 9α AND 12α HALOPROGESTERONES



		Liver glycogen rat cortisone acetate = 1		Sodium retention rat DCA = 1	
9α or 12α Halo en	Y	9α	12α	9α	12α
Br	β OH	0 08 (0 02 0 29)	0 40 (0 25–0 64)	<0 02	<0 07
Br	Keto	0 03	<0 1	<0 02	<0 02
Cl	β OH	0 35 (0 27–0 44)	0 47 (0 33–0 54)	<0 07	0 1
Cl	Keto	0 15 (0 09–0 24)	<0 15	—	—
F	β OH	0 85 (0 69–1 04)	0 70 (0 48–1 04)	1 1	0 6
F	Keto	1 10 (0 87–1 38)	0 60 (0 38–0 95)	2 8	—

The figures in parentheses represent the 95 per cent confidence intervals calculated by the method of C I Bliss

and testosterone Thus 9α fluorination has again enhanced the biological activity of the parent substance TABLE 2 also shows data for the more highly hydroxylated products 9α fluoro 11β 17α dihydroxyprogesterone and 9α fluorohydrocortisone which particularly in the normal animal indicate reduced potency as a result of side chain hydroxylation Huggins and Jensen noted that the histological changes in the vaginal epithelium following administration of 9α fluoro 11β hydroxyprogesterone were reminiscent of the changes with progesterone itself Hertz and Tullner [8] using the Clauberg

TABLE 2
INHIBITION OF GROWTH OF THE UTERUS BY
9α FLUORINATED STEROIDS[7]

Steroid	Estrone 0.5 μg hypox rat		Intact immature rat		Testosterone 1 mg hypox rat	
	Dose (μg)	Per cent inhibition	Dose (μg)	Per cent inhibition	Dose (μg)	Per cent inhibition
Progesterone	250	36	200	27	1000	5
11β Hydroxyprogesterone	1000	22	200	21	1000	32
9α Fluoro-11β hydroxy progesterone	250	51	100	44	100	35
9α Fluoro 11β 17α dihydroxy progesterone	—	—	100	24	250	38
9α Fluorohydrocortisone	250	51	100	18	250	36

technique were indeed able to demonstrate classic progesteronelike activity for this halogenated steroid. Their results are summarized in TABLE 3. Comparison of the figures for 11β hydroxyprogesterone with those for its 9α fluoro derivative shows an increase in activity due to halogenation by a factor of 5 to 10. Similar enhancement is seen with 9α fluorohydrocortisone and 9α chlorohydrocortisone which possess low yet significantly higher activity than hydrocortisone.

In an effort to ascertain the effects of the different halogens on antiuterotrophic and progestational activity we have extended the studies cited above to include all the 9α and 12α halo 11β hydroxyprogesterones and 11 ketoprogesterones. The test employed for the evaluation of antiuterotrophic potency has been described in the preceding paper and the results

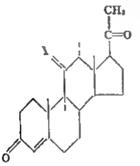
TABLE 3
PROGESTATIONAL ACTIVITY OF 9α HALO STEROIDS
IN THE CLAUBERG ASSAY

Steroid	Activity (progesterone = 1)
Progesterone	1.00
11β Hydroxyprogesterone	0.01
9α Fluoro-11β hydroxyprogesterone	0.05–0.10
9α Fluoro-11β 17α dihydroxyprogesterone	0.05–0.10
9α Fluorohydrocortisone	0.03
9α Chlorohydrocortisone	0.03
9α Fluoro 1 dehydrohydrocortisone	<0.02
Hydrocortisone	<0.01

Data from Hertz and Tullner[8]

obtained are summarized in TABLE 4. The potencies of the different compounds are expressed in terms of the dosage required for 25 per cent inhibition of the uterine response to 0.03 μg of estradiol. Increase in dosage leads to increased inhibition which, however, in no case exceeds 80 per cent. In comparing the potencies of the various derivatives it is at once evident that the structure-activity relationships established for corticoid activity

TABLE 4
ANTI-UTEROTROPHIC ACTIVITY OF 9α AND 12α HALOPROGESTERONES IN THE IMMATURE MOUSE



9α or 12α Halogen	X	Dose required for 25 per cent inhibition* of the uterotrophic response elicited by 0.03 μg estradiol (μg.) 9α	12α
I	β OH	0.5–1.0	5–25
I	Keto	—	25–125
Br	β OH	15–30	10
Br	Keto	5.0–10	>450
Cl	β OH	20	2.5–5.0
Cl	Keto	1.0	450
F	β OH	5.0–10.0	20
F	Keto	5.0–10.0	<50
Progesterone		2–10	—

* Per cent inhibition $= 100 - \left[\frac{(\text{halosteroid} + \text{estradiol}) - \text{control}}{\text{estradiol} - \text{control}} \times 100\right]$

no longer obtain in this case. The activities of all the 9α halo derivatives lie in the same range, which is approximately equal to that found for progesterone. This is true also for the 12α halo series with the exception that the 12α bromoketone is inactive and that the chloroketones and iodoketones possess considerably lower activities than their hydroxy analogues. This latter phenomenon, which incidentally is also observed with these compounds in the liver glycogen and Clauberg assays, is believed to be due to the reduced rate of conversion of the inactive ketones to the active 11β

PART V ACCESSORY READING

LIST OF ILLUSTRATIONS

PART I

INTRODUCTORY AND HISTORICAL

CHAPTER I

INTRODUCTION

WHAT ORGANIC EVOLUTION IS—DEFINITIONS

The following selections are representative both of the older and of the newer attitudes of thinkers on the subject of organic evolution The earlier writers were greatly impressed with the sublimity of the idea and found it in full accord with their religious faith The later writers are less awed by the vastness of the process and hence adopt a more completely materialistic attitude It is not necessary how ever to discard one s religious beliefs in order to adopt a scientific attitude toward the problems of organic evolution These points of view are well expressed in the following quotations

The world has been evolved not created it has arisen little by little from a small beginning and has increased through the activity of the elemental forces embodied in itself and so has rather grown than suddenly come into being at an almighty word What a sublime idea of the infinite might of the great Architect! the Cause of all causes the Father of all fathers the *Ens entium!* For if we could compare the Infinite it would surely require a greater Infinite to cause the causes of effects than to produce the effects themselves

' All that happens in the world depends on the forces that prevail in it and results according to law but where these forces and their substratum Matter, come from we know not and here we have room for faith —Erasmus Darwin as interpreted by Weismann

When I first came to the notion of a succession of extinction of species and creation of new ones going on perpetually now and through an indefinite period of the past and to continue for ages to come all in accommodation to the changes which must continue in the inanimate and habitable earth the idea struck me as the grandest which I had ever conceived so far as regards the attributes of the Presiding Mind —From a letter of Sir Charles Lyell to Sir John Herschel 1836

See Joseph Le Conte *Relation of Evolution to Materialism* Appendix.

From R. S Lull *Organic Evolution* (The Macmillan Company Reprinted by permission)

'It is interesting to contemplate a tangled bank, clothed with many plants of many kinds with birds singing on the bushes, with various insects flitting about and with worms crawling through the damp earth, and to reflect that these elaborately constructed forms, so different from each other and dependent upon each other in so complex a manner have all been produced by laws acting around us These laws taken in the largest sense being Growth with Reproduction Inheritance which is almost implied by reproduction, Variability from the indirect and direct action of the condition of life and from use and disuse a Ratio of Increase so high as to lead to a struggle for Life and as a consequence to Natural Selection, entailing Divergence of Character and the Extinction of less improved forms Thus from the war of nature from famine and death, the most exalted object which we are capable of conceiving namely the production of the higher animals directly follows There is a grandeur in this view of life with its several powers, having been originally breathed by the Creator into a few forms or into one and that while this planet has gone cycling on according to the fixed law of gravity, from so simple a beginning endless forms most beautiful and most wonderful have been and are being evolved —Charles Darwin *Origin of Species* concluding paragraph

Speaking broadly we find as a fact that transmutation of species through the geologic ages has been accompanied by increasing divergence of type by the increased specialization of certain forms and by the closer and closer adaptation to conditions of life on the part of the forms most highly specialized the more perfect adaptation and the more elaborate specialization being associated with the greatest variety or variation in the environment Accepting for this process the name organic evolution Herbert Spencer has deduced from it the general law that as life endures generation after generation its character as shown in structure and function, undergoes constant differentiation and specialization. In this view, the transmutation of species is not merely an observed process but a primitive necessity involved in the very organization of life itself —D S Jordan and V L Kellogg, *Evolution and Animal Life* (1908) p 4

The Doctrine of Evolution is a body of principles and facts concerning the present condition and past history of the living and lifeless things that make up the universe It teaches that natural processes

have gone on in the earlier ages of the world as they do to-day and that natural forces have ordered the production of all things about which we know —Henry Edward Crampton *The Doctrine of Evolution* (1911) p 1

' Evolution is the gradual development from the simple unorganized condition of primal matter to the complex structure of the physical universe, and in like manner, from the beginning of organic life on the habitable planet, a gradual unfolding and branching out into all the varied forms of beings which constitute the animal and plant kingdoms The first is called Inorganic the last Organic Evolution —Richard Swann Lull *Organic Evolution* (1917), p 6

THE MODERN ATTITUDE AS TO THE TRUTH OF THE EVOLUTION DOCTRINE

"Among that public which though educated and intelligent is not yet professionally scientific there has been of late a widespread belief that naturalists have become very doubtful as to the truth of the theory of evolution and are casting about for some more satisfactory substitute, which shall better explain the infinitely varied and manifold character of the organic world This belief is an altogether mistaken one for never before have the students of animals and plants been so nearly unanimous in their acceptance of the theory as they are to-day It is true that there are still some dissentient voices as there have been ever since the publication of Darwin s Origin of Species but the whole trend of scientific opinion is strongly in favor of the evolutionary hypothesis ' —William Berryman Scott, *The Theory of Evolution* p 1

' But the biological sciences were still slower [than the physical sciences] to come to their true position as dignified science Here was the last stronghold of the supernaturalist. Thrust out from the field of physical science it was in the phenomena of life that the last stand was made by those who claim that supernatural agency intervenes in nature in such a way as to modify the natural order of events When Darwin came to dislodge them from this their last intrenchment there was a fight intense and bitter but, like all attempts to stay the progress of human knowledge this final struggle of the supernaturalists was foredoomed to failure The theory of evolution has taken its place beside the other great conceptions of natural relations and largely through its establishment biology has become truly a science

with a large group of phenomena consistently arranged and properly classified The di cussion which followed the publication of Darwin's Origin of Species lasted for nearly a generation but it is now practically closed so far as any attempt to discredit evolution as a true scientific generalization is concerned Scientists are no longer questioning the fact of evolution they are busied rather with the attempt to further explore and more perfectly understand the operation of the factors that are at work to produce that development of animals and plants which we call organic evolution —Maynard M Metcalf, *An Outline of the Theory of Organic Evolution* (1911) pp xxii–xxiii

Biologists turned aside from general theories of evolution and their deductive application to special problems of descent in order to take up objective experiments on variation and heredity for their own sake This was not due to any doubts concerning the reality of evolution or to any lack of interest in its problems It was a policy of masterly inactivity deliberately adopted for further discussions concerning the causes of evolution had clearly become futile until a more adequate and critical view of existing genetic phenomena had been attained —E B Wilson (address as president of the American Association for the Advancement of Science 1914)

' The theory of development as it was revived by Darwin nearly half a century ago is in its modern form prevailingly unhistorical True it has forced beneath its sceptre the methods of investigation of all the sciences which deal with the living world and to-day almost completely controls scientific thought And yet science does not sincerely rejoice in its conquests Only a few incorrigible and uncritically disposed optimists steadfastly proclaim what glorious progress we have made otherwise in scientific as in lay circles, there prevails a widespread feeling of uncertainty and doubt Not as though the correctness of the principle of descent were seriously questioned rather does the conviction steadily grow that it is indispensable for the comprehension of living nature, indeed self evident —Gustav Steinmann (translated by W B Scott from *Die Abstammungslehre* [1908], pp 1–2)

The many converging lines of evidence point so clearly to the central fact of the origin of forms of life by an evolutionary process that we are compelled to accept this deduction, but as to almost all the essential features whether of cause or of mode by which specific

diversity has become what we perceive it to be we have to confess an ignorance nearly total —William Bateson *Problems of Genetics* (1913), p 248

' The demonstration of evolution as a universal law of living nature is the great intellectual achievement of the nineteenth century Evolution has outgrown the rank of a theory for it has won a place in natural law beside Newton s law of gravitation, and in one sense holds a still higher rank, because evolution is the universal master while gravitation is among its many agents Nor is the law of evolution any longer to be associated with any single name not even with that of Darwin, who was its greatest exponent It is natural that evolution and Darwinism should be closely connected in many minds but we must keep clear the distinction that evolution is a law while Darwinism is merely one of the several ways of interpreting the workings of this law

"In contrast to the unity of opinion on the law of evolution is the wide diversity of opinion on the *causes* of evolution In fact the causes of the evolution of life are as mysterious as the law of evolution is certain Some contend that we already know the chief causes of evolution others contend that we know little or nothing of them In this open court of conjecture of hypothesis of more or less heated controversy the names of Lamarck, of Darwin of Weismann figure prominently as leaders of different schools of opinion while there are others like myself, who for various reasons belong to no school and are as agnostic about Lamarckism, as they are about Darwinism or Weismannism or the more recent form of Darwinism termed Mutation by De Vries

In truth from the period of the earlier stages of Greek thought man has been eager to discover some natural cause of evolution and to abandon the idea of supernatural intervention in the order of nature Between the appearance of *The Origin of Species* in 1859, and the present time there have been great waves of faith in one explanation and then in another each of these waves of confidence has ended in disappointment until finally we have reached a stage of very general scepticism Thus the long period of evolution experiment, and reasoning which began with the French natural philosopher Buffon one hundred and fifty years ago ends in 1916 with the general feeling that our search for causes far from being near completion has only just begun

Our present state of opinion is this we know to some extent *how* plants and animals and man evolve we do not know *why* they evolve We know for example that there has existed a more or less complete chain of beings from monad to man that the one-toed horse had a four toed ancestor that man has descended from an unknown ape-like form somewhere in the Tertiary We know not only those larger chains of descent, but many of the minute details of these transformations. We do not know their internal causes for none of the explanations which have in turn been offered during the last hundred years satisfies the demands of observation, of experiment, of reason. It is best frankly to acknowledge that the chief causes of the orderly evolution of the germ are still entirely unknown and that our search must take an entirely fresh start. —H. F Osborn, *The Origin and Evolution of Life* (Charles Scribner s Sons), 1918 pp viii–x.

WHAT ORGANIC EVOLUTION IS NOT

1 The evolution doctrine is not a creed to be accepted on faith as are religious faiths or creeds. It appeals entirely to the logical faculties not to the spiritual, and is not to be accepted until proved.

2 It does not teach that man is a direct descendant of the apes and monkeys but that both man and the modern apes and monkeys have been derived from some as yet unknown generalized prima[te] ancestor possessing the common attributes of all three groups and lacking their specializations.

3 It is not synonymous with Darwinism, for the latter is merely one man s attempt to explain how evolution has occurred.

4. Contrary to a very widespread idea, evolution is by no means incompatible with religion. Witness the fact that the early Christian theologians, Augustine and Thomas Aquinas, were evolutionists and the majority of thoughtful theologians of all creeds are today in accord with the evolution idea, many of them even applying the principle to their studies of religion for religious ideas and ideals, like other human characters, have evolved from crude beginnings and are still undergoing processes of refinement.

5. The evolution idea is not degrading Quite the contrary it is ennobling as is well brought out by the classic statement of Darwin on page 4 and by that of Lyell, on page 3

6. The evolution doctrine does not teach that man is the goal of all evolutionary process, but that man is merely the present end product of one particular series of evolutionary changes. The goal

of evolution in general is perfection of adaptation to the conditions of life as they happen to be at any particular time Many a highly perfected creature has reached the goal of its evolutionary course only to perish because it was too highly perfected for a particular environment and could not withstand the hardships incident to radically changed world-conditions Many evolutions therefore have been completed while others are still awaiting the opportunity to speed up toward a new goal

7 Evolution is therefore not entirely a thing of the past Obviously some species including Man perhaps are nearly at the end of their physical evolution but there are always certain generalized plastic types awaiting the next great opportunity for adaptive specialization

CHAPTER II

HISTORICAL ACCOUNT OF THE DEVELOPMENT OF THE EVOLUTION THEORY

The chief sources of material for the present chapters are Osborn's *From the Greeks to Darwin* and Judd's *The Coming of Evolution*.

Professor Osborn studies the evolution of the evolution idea as a biologist would investigate the evolution of a group of species using all of the available sources of evidence at his disposal. The fragments of ancient writing and the crude imaginings of early natural philosophers are the fossils of the evolution idea many of them ancestors of modern principles; fragments of ancient or discarded ideas that still persist, though irrelevant to modern thought, are the vestigial structures that proclaim kinship between the past and the present, parallelisms between the development of ideas in the minds of independent thinkers do not prove plagiarism but indicate common descent from the same ancestral ideas.

This whole history is an important chapter in the story of human evolution in general for it deals with the evolution of a characteristic human faculty—that of appreciating the broad relations that exist between the past and the present. This faculty has evolved as truly as has an organic system such as the nervous system and is unquestionably closely bound up with the latter.

The evolution theory is a vast fabric of interrelated and interdependent facts and principles. The fabric has been gradually woven out of separate threads and now stands strong though flexible with strands reaching into all sciences and tending to unify all science.

It was only after the lesser ideas came to be clearly apprehended that it was possible for the master minds of Lamarck and of Darwin to weave them together into a consistent fabric and to bring the facts together under the one great conception that of organic evolution. Classification was a science, comparative anatomy had made much progress, the principles of embryology were fairly well understood.

H F Osborn *From the Greeks to Darwin* (The Macmillan Company 1908)

John W Judd *The Coming of Evolution* (Cambridge University Press 1911)

much palaeontological discovery had been made, before it was found that the facts from these sources all pointed to one general principle and only one that master principle ' organic evolution

We shall now trace the development of the evolution idea from its inception among the Greeks to its present status and shall first give a brief account of Greek evolution

EVOLUTION AMONG THE GREEKS

The early Greek thinkers were sea people "Along the shores and in the waters of the blue Aegean,' says Osborn ' teeming with what we now know to be the earliest and simplest forms of animals and plants they founded their hypotheses as to the origin and succession of life The spirit of the Greeks was vigorous and hopeful Not pausing to test their theories by research they did not suffer the disappointments and delays which come from one s own efforts to wrest truths from Nature

The Greeks were anticipators of Nature Their speculations out stripped the facts in fact were usually made with eyes closed to the facts Their theories were inextricably bound up with current mythology were naive, vague and from our modern point of view ridiculous yet they contained many grains of truth and were the germs out of which grew the saner ideas of subsequent thinkers

Thales (624–548 B C) was the first of the Greeks to theorize about the origin of life He looked upon the great expanse of mother ocean and declared water to be the mother from which all things arose and out of which they exist *This idea anticipates the modern idea of* the aquatic or marine origin of life, and also the present idea as to the indispensability of water in all vital processes

Anaximander (611–547 B C) has been called the prophet of Lamarck and of Darwin While his theories were highly mythical in character, he conceived the idea of a gradual evolution from a formless or chaotic condition to one of organic coherence He saw vaguely the idea of *transformation of aquatic species into terrestrial* even deriving man from aquatic fishlike men (mythical mermen) who were able to emerge from the water only after they had undergone the necessary changes required for land life This idea involves that of *adaptation* one of the cornerstones of the modern evolutionary structure

Anaximenes (588–524 B C) a pupil of Anaximander, found in air the cause of all things Air, taking the form of soul imparts life motion and thought to animals " It is questionable whether this is a

prophecy of the importance of oxygen and oxidation in vital processes Anaximenes also introduced the idea of abiogenesis (spontaneous generation of living sub tance) his idea being that animals and plants arose out of a *primordial terrestrial slime* wakened into life by the sun s heat This primordial terrestrial slime is perhaps a prophecy of Oken s Urschleim or of protoplasm

Xenophanes (576–480 B C) probably another pupil of Anaximander agreed with his master so far as to trace the origin of man back to the transition period between the fluid or water and solid or land stages of the development of the earth He was the first to recognize *fossils* as the remains of animals once alive, and to see in them proof that once the seas covered the entire surface of the earth.

Heraclitus (535–475 B C) the first of a group of physicists was the great proponent of the philosophy of change He was imbued with the idea that all was motion that nothing was fixed "Everything was perpetually transposed into new shapes Although Heraclitus did not apply his ideas to living creatures and their evolutions his philosophy was influential in molding the ideas of his successors

Empedocles (495–435 B C) took a great stride beyond his predecessors and may justly be called the father of the Evolution idea He believed in Abiogenesis or spontaneous generation, as the explanation of the origin of life but that Nature does not produce the lower and higher forms simultaneously or without an effort Plant life comes first and animal life developed only after a long series of trials He thought that all creatures arose through the fortuitous combination of scattered and miscellaneous parts which were attracted or epelled by the forces of love or hate (the two great forces in Nature) Thus arose every sort of combination of parts some more or less harmonious and complete others with ill assorted organization lacking in some parts double or triple in others Some of these combinations could not survive because of their incompleteness and incongruity but ' other forms arose which were able to support themselves and multiply This is a sort of vague prophecy of the survival of the fittest or of natural selection Four sparks of truth may be found in Empedocles philosophy first that the development of life was a gradual process second that plants were evolved before animals third, that imperfect forms were gradually replaced (not succeeded) by perfect forms fourth that the natural cause of the production of perfect forms was the extinction of the imperfect

Democritus (b 450 B C) said to have been the first comparative anatomist, contributed to the substructure of evolution the idea of the ' adaptation of single structures and organs to certain purposes

Anaxagoras (500–428 B C) was the first of the Greeks to attribute the adaptations of Nature to Intelligent Design, and was thus the founder of Teleology ' an idea that has played a retarding function in the history of evolution

With *Aristotle* (384–322 B C) we enter a new world, says Osborn He towered above his predecessors and by the force of his genius created Natural History ' The evolution idea took a great step forward with Aristotle and reached a stage beyond which it did not go for many centuries He covered nearly the whole field touching upon most of the foundation stones of the complex problem His ideas like those of all the Greeks were often vague and in the light of present knowledge incoherent but, considering the meager factual background with which he had to work he had a surprising grasp of the whole situation Some of his principal ideas were

1 He had a clear idea of laws of Nature (Necessity) and attributed all evolutionary changes to natural causes

2 He opposed the ideas of Empedocles as to the fortuitous origin of adaptive characters and favored the idea of intelligent design in nature He was therefore a teleologist

3 Hence he rejected the hypothesis of the survival of the fittest because it was based on chance

4 He had substantially the modern conception of the Evolution of life from a primordial soft mass of living matter

5 He had an idea of a linear phylogenetic series beginning with plants then plant animals such as sponges and sea anemones then animals with sensibility and thence by graded stages up to Man

6 He perceived the unity of type in certain classes of animals and considered rudimentary organs as tokens whereby Nature sustains this unity

7 He anticipated Harvey s doctrine of Epigenesis in embryonic development

8 He fully perceived the forces of hereditary transmission of the prepotency of one parent or tock, and of Atavism and Reversion

9 He is the father of that ancient fallacy called prenatal influ ences ' and believed in the inheritance of acquired characters as is shown in the following passage

"Children resemble their parents not only in congenital characters, but in those acquired later in life For cases are known where parents have been marked by scars and children have shown traces of these scars at the same points a case is also reported from Chalcedon in which a father had been branded with a letter and the same letter somewhat blurred and not sharply defined appeared upon the arm of the child"

POST ARISTOTELIANS

With Aristotle the evolution idea reached a high watermark and thereafter the tide steadily declined Pliny Epicurus Lucretius, and others kept the idea alive, but added nothing of importance to Aristotle s contribution

Lucretius (99–55 B C) appears to have been chiefly a follower of Empedocles in so far as his ideas as to the origin of animals are concerned He ignored Aristotle and his much more advanced philosophy of Nature finding the earlier, more mythical conceptions better suited to poetic expression He was not truly an evolutionist for he believed that all animals and plants arose fully formed from the earth Lucretius is of importance chiefly as a retarding factor for his ideas were accepted and admired even up to the eighteenth century witness Milton s immortal verse

The Earth obey d, and straight
Op ning her fertile womb teem d at a birth
Innumerous living creatures perfect forms
Limb d and full grown

THE EARLY THEOLOGIANS

The evolution idea made no progress from the time of Aristotle until the revival of learning in the Middle Ages The chief inhibiting factor was the church, which favored traditional knowledge and the special-creation idea in its most literal form Yet the early theologians such as Gregory Augustine and Thomas Aquinas were open minded about the evolution idea and attempted to reconcile it with the scriptural account of creation

'*Gregory of Nyssa* (331–396 A D) taught," says Osborn that Creation was potential God imparted to matter its fundamental properties and laws The objects and completed forms of the Universe developed gradually out of chaotic material!

Augustine (353–430 A D) conceived the idea, now so generally adopted by theologians, that the biblical account of creation is allegorical In explaining the passage 'In the beginning God created heaven and the earth' he says

'In the beginning God made the heaven and the earth, as if this were the *seed* of the heaven and the earth although as yet all the matter of heaven and of earth was in confusion, but because it was certain that from this the heaven and the earth would be therefore the material itself is called by that name '

Thomas Aquinas (1225–74) who wrote much later and was one of the leading church authorities satisfied himself with merely expounding Augustine 'As to the production of plants Augustine holds a different view, for some say that on the third day plants were actually produced, each in its kind—a view favoured by the superficial reading of Scripture But Augustine says that the earth is then said to have brought forth grass and trees *causaliter*, that is it then received the power to produce them For in those first days God made creation primarily or *causaliter* and then rested from His work.

THE REVIVAL OF SCIENCE

During the long centuries until the awakening of science in the Middle Ages the evolution idea smouldered along in the minds of a few thinkers but it was only when a few daring spirits broke the trammels of scholasticism and began once more to give free rein to observation and speculation that the idea once more burst into flame and began its second great period of advance

A small group of natural philosophers scarcely more scientific in their methods than the Greeks were the first to revive interest in the evolution idea Of these the names of Bacon Descartes Leibnitz and Kant are the most famous

Francis Bacon (1561–1626) did much to revive the vogue of Aristotelian ideas He also added some new ideas (1) that the mutability of species was the result of the accumulation of variations (2) that variations of an extreme kind equivalent to mutations, sometimes occur (3) that new species might arise by a degenerative process from old species

Emmanuel Kant (1724–1804) was purely a philosopher, not an observing naturalist but he profited by the writings of the contemporary naturalists especially those of Buffon and Maupertuis His

general ideas of evolution were comprehensive and summed up the best features of all preceding writers but he did not contribute any thing new to the pressing problem of the causes of evolution

Real progress was not to be made through further speculation What was most needed was facts and it was the task of the naturalists to furnish these The earliest of the eighteenth-century naturalists were still anticipators of Nature in that their theories outran their facts Of these the names of Bonnet and Oken are the best known

Bonnet (1720–93) was an evolutionist only in the sense that he believed that the adult organism is present in the egg and evolves from it by a process of unfolding or expansion He was a zoological observer of some note however and made some of the most important contributions of his time to the general subject He believed ' that the globe had been the scene of great revolutions and that the chaos described by Moses was the closing chapter of one of these, thus the Creation described in Genesis may be only a resurrection of animals previously existing This theory admits of no progress and is scarcely worthy of the name evolution

Oken (1776–1851) is known chiefly for his Urschleim doctrine and his ideas of cells as vesicular units of life According to him ' Every organic thing has arisen out of slime and is nothing but slime in various forms This primitive slime originated in the sea from inorganic matter ' These ideas are purely speculative but suggest our modern ideas of protoplasm and cells

THE GREAT NATURALISTS OF THE EIGHTEENTH CENTURY

Three great names stand out above all the rest during this period those of Linnaeus Buffon and Erasmus Darwin

Linnaeus (1707–78) was the father of taxonomy He contributed facts rather than theories he invented our present system of binomial nomenclature of both animals and plants and a great many of his generic and specific names still persist Unfortunately he was an ardent advocate of the special-creation idea holding that all of the true species were created as they are known today except that new combinations may have arisen through hybridization or through degeneration His influence was great but was reactionary and proved a serious hindrance to the progress of the evolution idea

Buffon (1707–88) born the same year as Linnaeus has been recognized as the father of the modern applied form of the evolution idea He attempted to explain particular cases on an evolutionary

basis. He lived at a time when it was dangerous to express views that might be interpreted as unorthodox, and this may account for the apparent lack of conviction in his own ideas for he wavered between special creation and evolution His chief contribution is the idea of the direct influence of the environment in the modification of the structure of animals and plants and the conservation of these modifications through heredity This seems to imply that he believed in the inheritance of acquired characters He expressed himself as believing that climate has had a direct effect in the production of various races of man that new varieties of animals have been formed through human intervention (an idea implying artificial selection) that similar results are produced by geographic migration and through isolation He expressed the view that there is a great struggle for existence among animals and plants to prevent overcrowding and to maintain the balance of Nature This appears to be an anticipation of Malthus ideas on population which were so influential in shaping the theories of Charles Darwin and of Wallace

While many of his ideas appear to be highly advanced for his time, his special applications are open to serious criticism He reasons for example that the pig as it exists at present could not have been formed on any original complete and perfect plan but seems to have been formed as a compound from other animals It has useless parts which could hardly have been a part of a perfect plan as originally conceived He thought that the ass is a degenerate horse and the ape a degenerate man

On the whole Buffon was not a strong advocate of evolution and his influence was far from being as important as some recent writers appear to believe

Erasmus Darwin (1731–1802), grandfather of Charles Darwin was a physician, a naturalist and a minor poet Undoubtedly he transmitted to his grandson his thoughtful habit and love of science and was influential in shaping his ideas on evolution The elder Darwin's theories as to the causes of evolution closely paralleled those of Lamarck his distinguished contemporary in France but it is now very generally conceded that the ideas of the two men were independently derived from similar materials Erasmus Darwin laid little emphasis on the direct action of the environment which had been Buffon's main dependence and dwelt on the internal origin of adaptive characters "All animals" he said undergo transformations which are in part produced by their own exertions in response to

pleasures and pains and many of these acquired forms or propensities are transmitted to their posterity One could ask for no clearer statement of the idea that acquired characters are inherited

The fierceness of the struggle for existence was clearly recognized by Dr Darwin He considers that this struggle is beneficial to Nature as a whole because it checks the too rapid increase of life One step farther in the argument and he would have arrived at the idea of the survival of the fittest but he never took that step He agreed with the early Christian fathers in his belief that the powers of development were implanted within the first organisms by the Creator and that subsequent evolution of adaptive characters went on without further divine intervention The power of improvement rests within the creature s own organizations and is due to his own efforts The effects of these efforts he believes are transmitted to offspring so that there might be a cumulative effect throughout many generations of the results of effort

Erasmus Darwin was perhaps the first to express clearly the ideas that millions of years have been required for the processes of organic evolution and that all life arose from one primordial protoplasmic mass He writes as follows

From thus meditating upon the minute portion of time in which many of the above changes have been produced would it be too bold to imagine in the great length of time since the earth began to exist perhaps millions of ages before the commencement of the history of mankind, that all warm blooded animals have arisen from one living filament which the first great Cause imbued with animality, with the power of acquiring new parts attended with new propensities directed by irritations sensations volitions and associations and thus possessing the faculty of continuing to improve by its own inherent activity and of delivering down these improvements by generation to posterity world without end?

LAMARCK

Lamarck (1744–1829) the greatest of French evolutionists, is now looked upon as the founder of the complete modern Theory of Descent Osborn considers him the most prominent figure between Aristotle and Darwin One cannot compare his *Philosophie zoölogique* with all previous and contemporary contributions to the evolution theory or learn the extraordinary difficulties under which he laboured and that his work was put forth only a few years after he had turned

from Botany to Zoology without gaining the greatest admiration for his genius No one has been more misunderstood, or judged with more partiality by over or under praise The stigma placed upon his writings by Cuvier, who greeted every fresh edition of his words as a nouvelle folie' and the disdainful illusions to him by Charles Darwin (the only writer of whom Darwin ever spoke in this tone) long placed him in the light of a purely extravagant speculative thinker Yet as a fresh instance of the certainty with which men of science finally obtain recognition it is gratifying to note the admiration which has been accorded to him in Germany by Haeckel and others by his countrymen and by a large school of American and English writers of the present day to note further that his theory was finally taken up and defended by Charles Darwin himself and that it forms the very heart of the system of Herbert Spencer '

Lamarck's main theory of evolution was expressed by him in the form of his four ' laws

I Life by its proper forces continually tends to increase the volume of every body which possesses it and to increase the size of its parts up to a limit which brings it about.

II The production of a new organ in the animal body results from the supervention of a new want which continues to make itself felt and a new movement which this want gives rise to and maintains

III. The development of organs and their powers of action are constantly in ratio to the employment of these organs

IV Everything which has been acquired impressed upon or changed in the organization of individuals during the course of their life is preserved by generation and transmitted to new individuals which have descended from those which have undergone these changes

It is about the last ' law that the controversy rages for it upholds the idea that *acquired characters are inherited* now known as the Lamarckian doctrine

A somewhat more specific statement of Lamarck s theory of evolution may be summed up in the following list of factors which he considered as playing an essential rôle in evolution

1 Favorable circumstances attending changes of environment soil food, temperature etc supposed to act directly in the case of plants indirectly in the case of animals and man

2 Needs new physical wants or necessities induced by the changed conditions of life Lamarck believed that change of habits

may lead to the origination or modification of organs that changes of function also modify or create new organs By changes of environment animals become subjected to new surroundings involving new ways and means of living Thus certain land bird driven by necessity to obtain their food in the water gradually assumed characters adapting them for swimming wading or for searching for food in the shallow water as in the case of the long necked kinds

3 Use and disuse To use an organ is to develop it not to use it is to eventually lose it The anterior limbs of birds became capable of sustained flight through use the hind limbs of whales are lost through disuse etc

4 Competition Nature takes precautions not to overcrowd the earth The stronger and larger living things destroy the smaller and weaker The smaller multiply very rapidly the larger slowly A physiological balance is maintained

5 The transmission of acquired characters The advantages gained by every individual as the result of the structural changes resulting from use or disuse are handed down to its descendants who begin where the parent leaves off and so are able to continue the progression or retrogression of the character

6 ' Cross-breeding If when any peculiarity of form or any defects whatsoever are acquired the individuals in this case always pairing they will produce the same peculiarities and if for successive generations confined to such unions a special distinct race will then be formed But perpetual crosses between individuals which have not the same peculiarities of form result in the disappearance of all the peculiarities acquired by the particular circumstances

7 Isolation Were not man separated by distances of habitation the mixtures resulting from crossing would obliterate the general characters which distinguish different nations This thought is expressed in his account of the origin of men from apes and is not applied to living things in general

In addition to his theories as to the causes of evolution Lamarck was the first to present the idea of the tree of life or phylogenetic tree as a mode of representing animal relationships All previous classifications had been based on the idea of a single linear phylogenetic series each lower group being supposedly ancestral to a higher group and all in a single chain

We may best sum up Lamarck s work and influence in the words of Osborn

'Lamarck as a naturalist, exhibited exceptional powers of definition and description while in his philosophical writings upon Evolution, his speculation far outran his observations and his theory suffered from the absurd illustrations which he brought forward in support of it His critics spread the impression that he believed animals acquired new organs simply by wishing for them His really sound speculation in Zoology was also injured by his earlier thoroughly worthless speculation in Chemistry and other branches of science Another marked defect was that Lamarck was completely carried away with the belief that his theory of the transmission of acquired characters was adequate to explain all the phenomena He did not like his contemporaries, Erasmus Darwin and Goethe, perceive and point out that certain problems in the origin of adaptations were still left wholly untouched and unsolved His arguments are in most cases, not inductive, but deductive and are frequently found not to support his law but to postulate it

'It is now a question whether Lamarck's factor is a factor in Evolution at all! If it prove to be no factor Lamarck will sink gradually into obscurity as one great figure in the history of opinion If it prove to be a real factor he will rise into a more eminent position than he now holds —into a rank not far below Darwin

CUVIER AND GEOFFROY ST HILAIRE

Georges Cuvier (1769–1832) deserves especial mention as one of the strongest negative factors in the development of the evolution idea He was first of all an opponent of Lamarck and second of evolution in general He ranged himself with Linnaeus as a special creationist and advocated the idea of fixity of species All the beings said he belonging to one of these forms (perpetual since the beginning of all things that is the Creation) constitute what we call species' So able was Cuvier and so much in favor at the French court that he succeeded in throwing Lamarck's views into disrepute and thus greatly retarded the progress of evolution He was brilliant as a comparative anatomist and palaeontologist and will long be known for his discoveries in these fields

E Geoffroy St Hilaire (1772–1844) did his best to defeat the retarding influence of Cuvier The two engaged in a long and bitter controversy over the evolution idea While not a supporter of Lamarckism proper he was a thoroughgoing evolutionist favoring

the doctrine of *Buffon* that the direct action of the environment was the sole cause of evolution He also in a sense, anticipated De Vries in that he believed that new species might be formed by transmutation or sudden large variations occurring in one generation "Hence the underlying causes of transformations he said were profound changes induced in the egg by external influences, accidents as it were, regulated by law The controversy between Cuvier and St. Hilaire was a losing one for the latter The cards were stacked against him and after him the evolution idea was retired to comparative obscurity until revived by Charles Darwin

CATASTROPHISM AND UNIFORMITARIANISM

The development of the science of geology had a profound influence upon that of evolution The prevailing theories as to historical geology during the Middle Ages involved the idea of catastrophism According to this view all important changes in the earth s crust represented sudden radical transformations involving earthquakes volcanic outbursts floods sudden upliftings of submerged areas or equally sudden submergence of land bodies From these ideas naturally grew the related idea of great world wide destructions of animals and plants followed by re creation of new faunas and floras Cuvier for example interpreted the more or less distinct fossil strata as being the result of a series of tremendous cataclysms the last of which had been the great deluge of Scripture in which Noah figured prominently He thought that at each cataclysm great floods of water had covered the earth that the existing animals had been buried in mud and thus preserved as fossils and that a new creation followed each cataclysm The great strength of this conception was that it appeared to give scientific support to both special creation and the Mosaic account of the Flood As compared with the pure evolutionary conception this alternative was highly acceptable to the church and was proclaimed as orthodox The Scotch philosopher and geologist Hutton, who lived during the last half of the eighteenth century combated the idea of catastrophism by advocating the doctrine of uniformitarianism, a view involving the idea that past changes on the earth were the result of the same sort of gradual change as are observed to be taking place today—in brief that there has been a strict uniformity of change throughout the entire period of geologic history There may have been according to this view local catastrophes,

such as volcanic outbursts, earthquakes and floods but the main trend of change has been slow and constant due largely to erosion and allied phenomena This view had practically no influence on the ideas of the time and for a long period the idea of catastrophism triumphed over the more truly evolutionary view of uniformitarianism, thus the evolution idea was destined to lie dormant till revived by Charles Darwin

THE REAWAKENING OF THE EVOLUTION IDEA

A number of important influences paved the way for the rehabilitation of the evolution idea at the hands of the younger Darwin Which of these was the most important it is difficult to say Probably Charles Lyell s *Principles of Geology* and Malthus *On Population* were the most suggestive works that Darwin encountered He was also doubtless influenced by Robert Chambers *Vestiges of Natural History of Creation* which appeared in 1844

Charles Lyell (1797–1875) so successfully rehabilitated the doctrine of uniformitarianism in geology that it became very generally accepted thus paving the way for a more favorable consideration of the idea of organic evolution Charles Darwin as a very young man took Lyell s *Principles of Geology* with him on his voyage on the Beagle and read it with the greatest devotion as is evidenced by his dedication of the journal of his voyage ' To Charles Lyell Esq F R S, this second edition is dedicated with grateful pleasure as an acknowledgment that the chief part of whatever scientific merit this Journal and other works of the author may possess has been derived from studying the well known admirable *Principles of Geology*

Malthus influence on Darwin s ideas is well expressed by Judd as follows

Fifteen months after this systematic inquiry began [referring to Darwin s exhaustive working over of his notes taken during his voyage on the Beagle], Darwin happened to read the celebrated work of Malthus *On Population* for amusement and this served as a spark falling on a long prepared train of thought The idea that as animals and plants multiply in geometrical progression while the supplies of food and space to be occupied remain nearly constant and that this must lead to a struggle for existence of the most desperate kind was by no means new to Darwin for the elder De Candolle, Lyell and others had enlarged upon it yet the facts with regard to

the human race so strikingly presented by Malthus brought the whole question with such vividness before him that the idea of Natural Selection flashed upon Darwin s mind

CHARLES DARWIN (1809–82)

Charles Darwin is without question the foremost figure in the development of the evolution idea and probably in the development of science in general The publication of his book *The Origin of Species* in 1859 was the most important event in biological history As has been already shown Darwin s chief ideas had been anticipated not by one but by several of his predecessors Nevertheless he was the first to furnish a really adequate proof of the fact of evolution and his causo mechanical theory to explain the method of evolution was supported by a mass of systematically arranged data such as has been paralleled neither before nor since Darwin was the first evolutionist effectively to employ the inductive method that of everywhere seeking facts first and then devising theories to fit the facts He never allowed speculation to outstrip observation as nearly all of his predecessors had done but made theory await the amassing of facts in its support until the accumulation of the latter seemed almost to speak out the theory of themselves Our greatest debt to Darwin is due to his establishment of the factual basis of evolution his selection theory was relatively of minor significance in so far as its value in the development of the evolution idea was concerned Yet this latter theory gained the widest acceptance among the scientifically inclined during the entire post Darwinian period It has been viciously assailed on all sides and has tottered repeatedly under the attacks of well trained adversaries Some of the weaker elements of the theory have given way under stress and the whole selection factor as a primary causal factor in evolution has been seriously called into question but since Darwin s time *the fact* of evolution has been almost universally accepted

The story of Darwin s life is almost a romance Born in 1809 " says Lull this emancipator of human minds from the shackles of slavery to tradition saw the light of day upon the very day that ushered in the life of Abraham Lincoln the emancipator of human bodies from a no more real physical bondage Darwin studied first at Edinburgh but finding medicine unsuited to his tastes entered Christ s College Cambridge, as a candidate for the church His love

Richard Swann Lull *Organic Evolution* (The Macmillan Company 1917)

of Nature however dominated all other interests and shortly after graduation an opportunity came to join the ship Beagle' as naturalist in a voyage of exploration around the world The five years spent upon this memorable journey, the narrative of which is so admirably set forth in the book, *A Naturalist s Voyage around the World* resulted in the accumulation of the first of Darwin s great series of observations, the final decision to devote his life to zoological research and the beginning of that illness which made him a life long invalid This last factor necessitated a retired life and thus proved of indirect benefit as it enabled him to accomplish the immense amount of work which he did without being impeded by the distractions of a public career

SUMMARY OF DARWIN S THEORIES

Since two subsequent chapters are to be devoted to Darwinism only an outline of Darwin s theories need be presented in the present historical account

Although Darwin was an all round biologist and gave attention to practically every phase of evolutionary biology he is known especially for his *selection theories* There are three of these the theory of artificial selection the theory of natural selection, and the theory of sexual selection

a) *Artificial selection*—According to Darwin the commonest method of producing under human culture new races of animals and plants is that of selection The breeder selects from among the highly variable individuals of a parent race those which possess the beginnings of desired modifications and he breeds them together expecting that the offspring will show the desired character some in a more highly perfected condition others in a less The ones that vary favorably are again selected for breeding stock and the same process is carried on until the desired character has been perfected

Although we now know that this is far from being a typical experience among breeders it appeared to Darwin to be so typical that he transferred the selection idea from the breeder to Nature making Nature the selecting agency responsible for the production of natural wild species His argument is as follows

b) *Natural selection* —The following factors are involved

1 All animals and plants tend to multiply in geometrical ratio

2 There is not food or room for a much larger number of animals and plants than now exist

3 All members of a species vary in many if not all directions

4 Those that vary in the more favorable directions, so as better to fit them to meet the conditions of life survive in larger numbers than those varying in less favorable directions This is Spencer s survival of the fittest

5 The survivors of one generation become the parents of the next and therefore the more favorable characters are passed on more largely than the less favorable

6 There is in each generation a slow but definite approach toward complete adaptation to life conditions

7 Variations neither useful nor harmful would not be affected by natural selection and would be left either as fluctuating variations or as polymorphic characters

c) *Sexual selection* —This theory was offered to supplement that of natural selection because Darwin considered the latter as made quate to explain the facts of sexual dimorphism or secondary sexual characters The theory is as follows There is always a contest among males fo possession of females in which the inferior males are eliminated either because they are on the one hand less courageous or weaker or less well equipped with weapons of combat, or because on the other hand the more attractive males whether on account of colors odors phosphorescence behavior etc. would succeed in winning mat s from those less endowed Thus would be enhanced the sexual dimo phism until it reaches extremes in many cases that are truly remarkable

The name of *Alfred Russell Wallace* (1822–1913) will always be associated with that of Charles Darwin as co author of the theory of natural selection Wallace at the age of twenty six went on a naturalistic expedition primarily for collecting specimens from new regions He covered almost the same ground as did Darwin in his voyage on the Beagle Wallace had read Lyell s *Principles of Geology* Malthus *On Population* Chambers *Vestiges of Creation* While in Sarawak he tells us I was quite alone with one Malay boy as cook and during the evenings and wet days I had nothing to do but to look over my books and ponder over the problem which was rarely absent from my thoughts While thus engaged the idea of natural selection came to him as though by a sudden flash of insight When the idea was still in process of formation he wrote it out on thin paper and mailed it to Darwin stating that he considered the idea new and asking Darwin to show it to Lyell, who had expressed interest in a

former paper of Wallace The ideas were expressed under the title *On the Tendency of Varieties to Depart Indefinitely from the Original Type*, and it proved to be an unusually concise and lucid statement of the main points of the natural selection theory Darwin at once wrote to Lyell as follows

'I never saw a more striking coincidence if Wallace had my MS sketch written in 1842, he could not have made a better short abstract! Even his terms now stand as heads of my chapters Please return to me the MS which he does not say he wishes me to publish but I shall, of course, at once write and offer to send it to any journal So all my originality, whatever it may amount to will be smashed though my book, if it ever have any value will not be deteriorated as all the labour consists in the application of the theory I hope you will approve of Wallace s sketch, that I may tell him what to say

Lyell insisted that Darwin publish an abstract of his own work simultaneously with that of Wallace and this course was carried out Darwin s generosity was equaled by that of Wallace who wrote in 1870

I have felt all my life and still feel the most sincere satisfaction that Mr Darwin had been at work long before me and that it was not left for me to attempt to write *The Origin of Species* I have long since measured my own strength and know well that it would be quite unequal to the task '

Still later he wrote 'I was then (and often since) the young man in a hurry' he [Darwin] the painstaking student seeking ever the full demonstration of the truth he had discovered rather than to achieve immediate personal fame '

One must perforce admit the nobility of character of both men but there can be no serious competition between the two for the honor of being called the originator of the natural selection theory

CONTEMPORARY OPINION REGARDING THE VALIDITY OF DARWIN S VIEWS

At first Darwin was inclined to believe that the selection factor was all sufficient to account for the origin of species as well as that of adaptations but as time passed he modified his earlier more sanguine views and came to the conclusion that natural selection has been the main but not the exclusive means of modification ' Many of his followers went to such extremes in their advocacy of the all sufficiency of natural selection as would not have met with Darwin s approval

"The first effect of Darwin s works says McFarland,[1] "was to carry the world of science by storm but at the same time to arouse intense hostility on the part of the theologians who found the theory of descent incompatible with the doctrines of Creation In this conflict Darwin took no part but was championed by Huxley, while Bishop Wilberforce led the opposition The battle was long and bitter there was much acrimonious writing on both sides but the theory of descent—the doctrine of evolution—was found to be invulnerable and at present the theologians themselves have accepted it and even make use of it in their own work

But as the years flew by the Darwinian doctrines began to meet with assaults from the scientists themselves who having endeavored to prove their validity began to find them inadequate to the require ments of expanding knowledge The question was asked 'What is the origin of the fittest? Given the fittest we easily understand how it is perpetuated but how does it arise? In the striking phrase of someone Natural selection might explain the *survival* of the fittest but fails to account for the *arrival* of the fittest!

Darwin s main supporters during the most trying controversial period were Herbert Spencer and Thomas H Huxley

Herbert Spencer (1820–1903) was an extremely able supporter of the general theory of evolution but was more definitely an advocate of Lamarckism than of natural selection His rôle was that of a champion of the whole philosophy of evolution as opposed to special creation and it was largely due to his forceful writings that Darwinism won the battle against dogmatism Spencer tried to explain the structure of protoplasm (living substance) on a physicochemical basis He thought of the structural units of protoplasm as comparable with the molecules of chemical compounds each local region of the protoplasm in the organism being made up of different kinds of units which he called physiological units This conception of the physical basis of organic structure had a considerable influence in shaping Darwin s ideas and was probably the basis of the latter s provisional theory of pangenesis This theory was probably the first consistently worked out theory of the mechanics of heredity It was thought that every part of the body is continually giving off its particular kind of units (gemmules) into the blood These gemmules are transported by the blood stream to all parts of the body and

[1] J McFarland, *Biology General and Medical* (The Macmillan Company 1918)

collect in the germ cells The [illegible]
that from the germ cell will de[illegible]
various details If a part of [illegible]
tioning or through changed en[illegible]
gemmules, which in turn, wo[illegible]
the modification to the next ge[illegible]
factory even to Darwin and is now [illegible]

Spencer is best known in the his[illegible]
ardent neo-Lamarckian He states [illegible]
function produces change of structu[illegible]
changes of structure so produced a[illegible]
until it was cast down by Weismann.

Thomas Henry Huxley (1825–95) [illegible]
cal thinkers of the nineteenth century [illegible]
doctrine of evolution against Bishop W[illegible]
an able investigator in the fields of com[illegible]
ology At the British Association at O[illegible]
after an American professor had m[illegible]
fortuitous concourse of atoms? as a co[illegible]
Dr Samuel Wilberforce the Bishop of O[illegible]
flippant attack on the *Origin* by enquiring of [illegible]
as Darwin's champion if it 'was throu[illegible]h h[illegible]
mother that he claimed his descent from a [illegible]

'Huxley made the famous and well-de[illegible]
and I repeat—that a man has no reason to [illegible]
ape for his grandfather If there were a[illegible]
feel ashamed of recalling it would rather b[illegible]
and versatile intellect—who not content w[illegible]
of activity plunges into scientific questio[illegible]
acquaintance, only to obscure them by a[illegible]
the attention of his hearers from the real [illegible]
digressions and skilled appeals to religiou[illegible]

Huxley himself accepted the theory of
not without some important reservations—[illegible]
prevent him from becoming its most arden[illegible]
Darwin used to acknowledge Huxley's grea[illegible]
taking the defense of the theory—a defens[illegible]
controversy and state of health made him [illegible]
by laughingly calling him my general age[illegible]
replying to the critics declared he was Da[illegible]

Ernst Haeckel (1834–1919) was one of the earliest and most influential followers of Darwin in Germany In his *Generelle Morphologie* published in 1866 seven years after the *Origin of Species* first appeared he applied the doctrine of evolution and especially the theory of natural selection to the whole field of vertebrate morphology Beyond question Haeckel overapplied the theory and in a sense weakened its influence by his rather uncritical use of materials *His writings have been translated into most languages and* ' are popularly believed to represent the best scientific thought on the matter Biologists today however, are apt to look askance at Haeckel s works and to consider that they did more harm than good to Darwinism

August Weismann (1834–1914) was the first really original evolutionist after Darwin Like other thinkers of his time, he realized that further progress in the knowledge of the causal basis of evolution lay in further investigation of the causes of variation and the physical basis of heredity Weismann has been classed as a neo-Darwinian because he was a strong advocate of some form of selection but his ' selection was not the selection of Darwin Realizing that the greatest weakness of the natural selection theory lay in its inadequacy as an originator of variations he proposed the germinal-selection theory He contended that all heritable variations have their origin in the germ cell and therefore that a new type of organism arises only from a changed type of germ cell The germinal selection theory stands out in striking contrast with Darwin s pangenesis theory The former is centrifugal the latter centripetal Determiners of new characters according to Weismann arise in the germ plasm and work outward to all parts of the developing body while the 'gemmules Darwin s equivalent of determiners originate in the body tissues and are carried to the germ cells in each generation According to Weismann there is a struggle among the determiners for the available food and favorable positions in the germ cell and those that receive the most food and the best positions gain an initial advantage so that they are able to initiate the development of larger or more perfectly adapted organs The descendants through cell division of these favored determiners are in a position to compete with other determiners on a more favorable footing in each succeeding generation, so that the character represented by them steadily increases in a linear or definitely directed fashion *until it reaches the state of complete* adaptation or fitness Such a character *may* even continue its direct line of advance beyond the point of maximum fitness and result in

what are known as overspecializations The theory therefore would, if well founded account not only for the initial stages of new adaptive characters, but also for overspecializations, two phenomena that natural selection was unable to account for Not only were progressive evolutionary changes explained by germinal selection but regressive changes seemed to be even more readily accounted for on this basis In the struggle among determiners in the germ cell some of the less favored units would be handicapped at the outset by insufficient food or unfavorable position and would produce smaller or less effective structures Progressively from generation to generation these weakened determiners would lose ground and become less and less successful in competition until they were weaklings among determiners and would be able to initiate only degenerate or vestigial structures or else would die out and lose their place altogether thus accounting for total losses of structures

This theory does not exclude natural selection but rather increases its importance, for every structure that arises to the threshold of utility or disutility meets the winnowing process of natural selection The fitter individuals survive in the long run and these perpetuate the germ cells in which the successful determiners reside

A slightly different explanation of degenerating structures involves the principle of panmixia According to this idea, changing environmental conditions may render certain adaptive organs of lessened value or of no value as would be the case in the eyes of cave animals In different individuals the eye determiners would vary in their success in competition with other determiners and since natural selection would no longer put a premium on perfect eyes, all grades of eyes would be equally inherited and gradually the poorer or degenerate eyes would become more numerous, till finally there would be no good eyes in the race Thus it will be seen that the germinal selection theory was auxiliary to natural selection and tended to support the latter at two of its weakest points But the supporting theory itself has the fundamental weakness of lacking a factual basis It is purely hypothetical and cannot be put to an experimental test Every time an objection to the theory was raised an auxiliary hypothesis was added to explain away the difficulty till finally it fell to the ground through sheer top-heaviness unable further to support its intricate structure of interrelated hypotheses

A much more valuable and lasting contribution of Weismann was his theory of ' germinal continuity and of the ' apartness of the germ plasm The whole theory has come to be known as the ' germ plasm

theory" which forms the framework of nearly all of our modern genetics According to this view the germ plasm is immortal in that it is perpetuated from generation to generation through the instrumentality of mitotic cell division each germ cell being the product of the division of a previous germ cell back to the first germ cell that arose at the dawn of life Thus a germ cell cannot be a product of the soma but the soma is the product of germ cells The soma loses its generalized characters and specializes in various ways Once specialized soma cells are believed to have lost their capacity to play a germinal rôle Specialization means mortality Thus the relationship between parent and offspring is not that the parent gives rise to the offspring but that the same germ plasm gives rise to both parent and offspring

The logical conclusion to which this line of reasoning leads is that the changes in the soma no matter how produced are helpless to produce any effect upon the germ plasm since germ cells come only from germ cells and not from soma cells Consequently Weismann led the assault against Lamarckism and won the day so conclusively that even in these modern times few biologists have the temerity to express aloud any definite belief in the inheritance of acquired characters Weismann's germ plasm idea is the cornerstone of modern genetics though there are some forward looking biologists who looking at things with a physiological bias cannot make themselves believe in the total independence of any tissue—even the sacred germ plasm

Weismann's influence was very great especially during the last decade of the nineteenth century and his theories gave rise to an immense amount of research chiefly of a cytological and embryological character

ISOLATION THEORIES

Among the theories subsidiary to natural selection as an aid to species forming are the various isolation theories One of the weaknesses inherent in natural selection had to do with the probable swamping out of new types by promiscuous breeding with the more numerous individuals of the older types Anything says *Metcalf* which divides a species into groups which do not freely interbreed, is said to segregate (isolate) the members of the species into these subdivisions.

Some American writers especially *Jordan* and *Kellogg* *Gulick* and *Crampton* have dealt with the isolation factor in evolution and believe

that it is a major factor of as great importance in species forming or nearly so as natural selection But the prevailing opinion seems to be that isolation is really a kind of selection, more like artificial selection than anything else, which separates out certain pure lines and prevents promiscuous interbreeding Various agents are known to produce isolation by erecting barriers to interbreeding between groups of individuals within a species These segregative factors may be geographical climatic, reproductive physiological, or, in plants, the result of soil diversity Thus a mountain range, on the two sides of which a species migrates effectively separates the species into two independent groups Heat cold, moisture etc. separate others. Reproductive incompatibility between new and older types is equally effective as is assortative mating of like with like Like natural selection isolation has nothing to do with the origin of new types but merely aids in the preservation of types when once formed Were there not spontaneous variations among animals and plants, there would be nothing to isolate Therefore isolation plays only an auxiliary rôle helping to preserve new races once they are formed

ORTHOGENESIS THEORIES

The orthogenetic evolution theories of various authors based upon the assumed occurrence of variations in determinate lines or directions (a restricted and determinate variation as compared with the nearly infinite, fortuitous, and indeterminate variation assumed in the selection theories) are of several types The mention of two will reveal pretty well the more important characters of all Not a few biologists have always believed in the existence of a sort of mystic special vitalistic force or principle by virtue of which determination and general progress in evolution is chiefly fixed Such a capacity, inherent in living matter seems to include at once possibility of progressive or truly evolutionary change Not all evolution is in a single direct line to be sure ascent is not up a single ladder or along a single geological branch but these branches are few (as indeed we actually know them to be however the restriction may be brought about) and the evolution is always progressive that is, toward what we from an anthropocentric point of view are constrained to call higher and higher or more ideal life stages and conditions

Other naturalists also seeming to see this source of determinate or orthogenetic evolution but not inclined to surrender their disbelief in vitalism, in forces over and beyond the familiar ones of the

physicochemical world have tried to adduce a definite causomechanical explanation of orthogenesis The best and most comprehensive types of this explanation are those essentially Lamarckian in principle, in which the direct influence of environmental conditions the direct reactions of the life stuff to stimuli and influences from the world outside are the causal factors in such an explanation But while every naturalist will grant that such factors do change and control in a considerable degree the life of the individual most see no mechanism or means of extending this control directly to the species

The above quoted paragraphs from Jordan and Kellogg[1] will serve to place before the reader the general ideas involved in the orthogenesis conception A brief account of the various special theories of orthogenesis follows

Carl von Nägeli's ideas of orthogenesis involve a belief in a sort of mystical principle of progressive development a something, quite intangible that exists in organic nature which causes each organism to strive for or at least make for specialization or perfect adaptation This idea of an inner driving and directing force reminds one of the entelechy of Driesch or Bergson's creative evolution' Nageli believed that animals and plants would have developed essentially as they have without any struggle for existence or natural selection This form of orthogenesis theory then is alternative to natural selection

Theodore Eimer's theory of orthogenesis is more scientific and less mystical than Nageli's He believed that lines of evolution were not miscellaneous and haphazard but were confined to a few definite directions determined at their initial stages not by natural selection but by the laws of organic growth aided by the inheritance of acquired characters A new character makes a beginning as would the first step in a slow chemical change or series of such changes, and it must go through to a fixed end under given conditions just as surely as does the chemical process Only when a given character or line of evolution results in the production of a very positive advantage or disadvantage to the species does natural selection step in to interfere with orthogenesis The causes of orthogenesis are said to lie in the effects of external influences climate, nutrition or the given constitution of the organism

Actual species-forming or the breaking up into specific units of the orthogenetic lines of change depends according to Eimer upon

[1] Jordan and Kellogg *Evolution and Animal Life* (D Appleton and Company)

three factors a standstill or cessation of development on the part of some lines sudden development by leaps (practically mutations) and hindrance or difficulty of reproduction (the type of thing that Romanes emphasized as physiological isolation ten years later) Eimer illustrated his theories by the evolution of color patterns in lizards and those on the wings of butterflies In both he believed that longitudinal stripes were primitive, that rows of dots followed these which were in turn followed by crossbands, reticular patterns and finally by solid coloration This hypothetical phylogenetic order is more or less closely paralleled by the ontogenetic order, in the lizards at least

It will be noted that Eimer s theory places natural selection in a subordinate position but does not dismiss it altogether as is done by Nageli It aids natural selection in explaining adaptations in that it furnishes for natural selection various characters of selective value which may be either perpetuated or eliminated according to their utility

E D Cope a leading American palaeontologist of the past century, had an orthogenetic theory involving his ideas of bathmism" (growth force), kinetogenesis' (direct effect of use and disuse and environmental influence) and archaesthetism' (influence of primitive consciousness) It may be said that his ideas were Lamarckian throughout In common with the majority of palaeontologists of later date—Osborn Williston Hyatt, Smith and others—Cope felt the need of some factor other than natural selection to explain the apparent steady progress of characters in definitely directed lines as seen in the fossils It is natural therefore that palaeontologists almost universally lay hold of both Lamarckian and orthogenesi ideas

Charles Otis Whitman who until his death over twenty years ago was considered the leading American zoologist had strong leanings toward orthogenesis In one of his few publications he says

' Natural selection orthogenesis and mutation appear to present fundamental contradictions, but I believe that each stands for truth and reconciliation is not far distant The so-called mutations of *Oenothera* are indubitable facts but two leading questions remain to be answered First are these mutations now appearing as is agreed, independently of variation nevertheless the products of variations that took place at an earlier period in the history of these plants? Secondly, if species can spring into existence at a single leap without the assistance of cumulative variations may they not also originate with such

assistance? That variation does issue a new species and that natural selection is a factor, though not the only factor in determining results is, in my opinion, as certain as that grass grows although we cannot see it grow Furthermore I believe I have found indubitable evidence of species-forming variation advancing in a definite direction (orthogenesis) and likewise of variations in various directions (amphigenesis) If I am not mistaken in this, the reconciliation for natural selection and orthogene is is at hand

In concluding this brief account of orthogenesis, it should be said that definitely directed evolution is now believed to be one of the laws of organic evolution but that we have no clear ideas as yet as to what are its underlying causes Therefore *orthogenesis is not a causo mechanical theory of evolution at all*

THE MUTATION THEORY OF DE VRIES

The theory of mutations is associated with the name of *Hugo De Vries* the well known Dutch botanist that of "heterogenesis with the name of *H Korchinsky* a Russian

Though Korchinsky anticipated De Vries by several years his work was not supported by the large amount of experimental data that characterized that of the great Dutch worker The relative claims for recognition as the founder of the mutation theory are almost on a par with those of Darwin and Wallace for the natural selection theory Both Darwin and De Vries held back their theories until they appeared to be adequately supported by personally collected facts

There is a striking parallelism between the ideas and conclusions of De Vries and those of Korchinsky and since this is true a résumé of De Vries s better known work will serve to give the essentials of the whole conception

De Vries began his genetic experiments by a study of the variations of plants in the field After learning their normal variability in nature he transferred them to the experimental garden and there attempted to improve them by selection He found that the improved living conditions due to better soil and cultivation induced a wider range of variability in size luxuriance and fecundity Such variations were plus or minus in their character fluctuating about a mean or average It was exactly this type of variability that Darwin emphasized as the raw material of evolution but De Vries found by experiment that selection had no permanent hereditary effect when based

to fluctuating variations since the latter were merely somatic responses on variable growth conditions This negative finding led him to renewed interest in discontinuous or saltatory variations as the only alternative to fluctuating or continuous variations

He looked far and wide among species of wild plants for a species that might exhibit a significant amount of saltatory variation and finally discovered in the evening primrose (*Oenothera lamarckiana*) what seemed to exhibit exactly the hoped for characteristics. This large, stately plant with conspicuous yellow blooms had escaped from cultivation and was growing wild in the fields In addition to a large number of plants that showed only minor differences among themselves De Vries found several individuals growing among the typical individuals which differed not merely in degree but in kind These were as different as distinct varieties and when the seeds were planted in the garden they bred true to their kind The only question now was whether they had actually arisen from typical parents To test this possibility seeds of several typical plants were planted in the garden, the result being not only a repetition of the peculiar types observed in the field, but of about a dozen other true breeding types with well marked differences from the parent species and among themselves.

These new types De Vries considered as new elementary species and he called them "mutants They came into existence suddenly in one generation and as a rule bred true Whatever factors were responsible for mutations, the seat of origin must have been in the germ cell and not in the soma Consequently they were inherited fully from the start The same mutations occurred in considerable numbers and in successive years In one case a given mutation occurred only once in eight years of observation Some mutants were robust and successful others were weak and incapable of living under natural conditions others were sterile On the basis of these results which are reported in detail in chapter xxvi De Vries came to the conclusion that evolution was based upon the sudden appearance of new varieties or elementary species and not upon the natural selection of fluctuating variations.

The mutation theory compared and contrasted with the natural selection theory—It will be recalled that the raw material upon which natural selection works is the minute individual or continuous variation that is universal in all living forms and is known to be largely somatic in character and due to differences in environment. Darwin

did not distinguish between somatic and germinal variations The essential feature of mutations is that they are germinal in origin and therefore come forth full fledged in the first generation arising from the changed germ Darwin recognized "saltatory variations' or 'sports which are mutations, but did not consider them of sufficiently frequent occurrence to furnish an adequate material for selection

De Vries, on his side, did not discard the principle of selection, but showed that selection acted as between mutants, serving to eliminate those which are unfit and allowing the sufficiently fit to survive alongside the parent types According to Darwin s view, the new types arose only at the expense of the old for only through the elimination of the old (less fit) types could the new types progress toward further fitness Darwin s view was ill suited to explain the origin of new distinct types because the process of selection proceeded by imperceptible steps De Vries s view gives us distinctly different, pure breeding types at once that, if isolated would be new elementary species from the first

In conclusion it may be said that the mutation theory was at first intended as a substitute for natural selection but that later the selection idea was adopted as a directive principle, guiding mutations toward adaptiveness

THE RISE AND VOGUE OF BIOMETRY

No historical account of the development of the evolution idea would be complete without a statement of the rôle played by biometry in the study of evolutionary data Biometry is the statistical study of variation and heredity During the last decade of the nineteenth century it became obvious to those who had followed the progress of the subject that farther advance toward the solution of the problem of the causes of evolution must come from a better understanding of variation and heredity, the two fundamental factors involved. Three main modes of attack were developed during these years the statistical (biometry), the experimental (chiefly breeding work), and the microscopical (cytology or the study of the minute structure of the germ cells)

Sir Francis Galton a cousin of Charles Darwin was the founder of biometry He applied certain already understood principles that had been developed mainly in the study of the laws of chance to the study of variations and by comparing the boiled down formulas

resulting from his computations of parental generations with those of offspring he arrived at two laws of heredity the law of filial regression and that of ancestral shares of inheritance The essence of the first was that the offspring of exceptional parents tend to regress toward mediocrity in proportion to the degree of parental exceptionalness The second law was really explanatory of the first, for it was found that the offspring inherit not only from parents but from the various grades of ancestors and it was the pulldown of a miscellaneous ancestry that made for regression toward mediocrity It appeared that half of the hereditary influence could be assigned to parents half of the remainder to grandparents, half of the remaining remainder to great grandparents, and so on down the line

Karl Pearson a pupil and follower of Galton, has carried the study of biometry to a more highly refined state. His attempt has been to apply to the study of evolution the precise quantitative methods which are used in physics and in chemistry While much of Pearson s work is far beyond the range of the average professional biologist today it is extremely useful as a tool in handling data in which great accuracy is demanded. Frequently, however, the methods are far too refined for the material and much time is wasted in handling crude data by means of highly refined instruments of measurement and ultra accurate mathematical methods

On the whole the contributions of biometry to our understanding of the causes of evolution are rather disappointing About the only clean-cut finding has been the discovery that some variations are continuous and others discontinuous The former are capable of being expressed in a single curve with a single mode while the latter are expressed in bimodal or polymodal curves If material is homogeneous to start with it is likely to give monomodal curves but if it is heterogeneous its heterogeneity will be revealed by the plural modes In a subsequent connection (chapter xliii) some further account of the details of biometry will be presented We must for the present be content with having placed biometry in its setting as one step in the advance of the evolution idea

EXPERIMENTAL BREEDING

"While De Vries says Castle was engaged in his studies of the evening primrose he hit upon an idea far more important as most biologists now believe than the idea of mutation, though De Vries

W E Castle *Genetics and Eugenics* (Harvard University Press 1920) p 81

himself, both before and since has seemed to regard it as of minor importance He called this the *law of splitting of hybrids* The same law it is claimed was independently discovered about the same time by two other botanists Correns in Germany and Tschermak in Austria Further historical investigations made by De Vries showed that the same law had been discovered and clearly stated many years previously by an obscure naturalist of Brunn Austria named *Gregor Mendel* and we have now come to call this law by his name *Mendel s Law* Mendel was so little known when his discovery was published that it attracted little attention from scientists and was soon forgotten, only to be unearthed and duly honored years after the death of its author Had Mendel lived forty years later than he did, he would doubtless have been a devotee of biometry, for he had a mathematical type of mind and his discovery of a law of hybridization was due to the fact that he applied to his biological studies methods of numerical exactness which he had learned from algebra and physics In biology he was an amateur being a teacher of the physical and natural sciences in a monastic school at Brunn Later he became head of the monastery and gave up scientific work, partly because of other duties, partly because of failing eyesight

There had been plant hybridizers before Mendel but their lack of exactness in technique had prevented them from discovering the law of segregation or splitting of hybrids

Joseph Gottlieb Kolreuter (1733–1806) who really belonged to the period of Lamarck barely missed making the discovery that was afterward made by Mendel The salient features of his work are according to Castle

' 1 Kölreuter established the occurrence of sexual reproduction in plants by showing that hybrid offspring inherit equally from the pollen plant and the seed plant

' 2 He showed that hybrids are commonly intermediate between their parents in nearly all characters observed such for example as size and shape of parts

3 Many hybrids are partially or wholly sterile especially when the parents are very dissimilar (belong to widely distinct species) Such hybrids often exceed either parent in size and vigor of growth

4 Kölreuter did not observe the regular splitting of hybrids which Mendel and De Vries record but some of his successors did particularly Thomas Knight (1799) and John Goss (1822) in England

Op cit., p 86

who were engaged in crossing the garden peas with a view to producing more vigorous and productive varieties and Naudin (1862) in France who made a comprehensive survey of the facts of hybridization in plants and came very near to expressing the generalization which Mendel reached four years later '

MENDEL S LAWS

The earliest experimental investigations of heredity," says Locy[1] in a concise summary of Mendel s work were conducted with plants, and the first epoch making results were those of Gregor Mendel (1822–1884) a monk and later abbot of an Augustinian monastery at Brunn Austria In the garden of the monastery for eight years before publishing his results he made experiments on the inheritance of individual (or unit) characters in twenty two varieties of garden peas Selecting certain constant and obvious characters as color, and form of seed, length of stem etc. he proceeded to cross these pure races thus producing hybrids and thereafter to observe the results of self fertilization among the hybrids

The hybrids were produced by removing the unripe stamens of certain flowers and later fertilizing them by ripe pollen from another pure breed having a contrasting character The results showed that only one of a pair of unit characters appeared in the hybrid of the next generation, while the other contrasting character lay dormant Thus in crossing a yellow seeded with a green seeded pea the hybrid generation showed only yellow seeds The character thus impressing itself on the entire progeny was called *dominant* while the other that was held in abeyance was designated *recessive*

' That the recessive color was not blotted out was clearly demonstrated by allowing the hybrid generation to develop by self fertilization Under these circumstances a most interesting result was attained The filial generation derived by self fertilization among the hybrids produced plants with yellow and green seeds but in the ratio of three yellow to one green All green seeded individuals and one third of the yellow proved to breed true while the remaining two thirds of the yellow seeded plants when self fertilized produced yellow and green seeds in the ratio of three to one

' Subsequent breedings gave an unending series of results similar to those obtained with the first filial generation.

[1] William A Locy *The Main Currents of Zoölogy* (Henry Holt & Company 1918) pp 37–39

"This great principle of alternative inheritance was exhibited throughout the extensive experiments of Mendel, and it is now recognized as one of the great biological discoveries of the nineteenth century

The essential feature of Mendel's discovery was not the phenomenon of dominance for relatively few instances of pure dominance have been discovered but it was the phenomenon of *segregation* By segregation is meant that although determiners for opposed hereditary characters derived from diverse parental sources may unite in a common germ plasm for one generation, they segregate out pure or unmodified by their association together, in the next and subsequent generations This law of segregation depends on the idea that the germ cell is composed of bundles of separately inheritable unit characters which may be paired or grouped, shuffled and redealt like cards, so as to give an infinite number of permutations and combinations without affecting the unit determiners themselves

From the evolutionary standpoint it is supposed that new unit characters arise by mutations and are fully hereditary They cannot be swamped out by interbreeding unless they are recessive for they will dominate the old characters Even recessive characters could be perpetuated by segregation or by the union of two individuals possessing the determiner in the recessive condition as well as the dominant Thus a knowledge of the behavior of unit characters in heredity reveals part of the mechanism for conserving new characters if they are advantageous or even sufficiently fit to survive

New types or species might arise through processes of hybridization and the survival of individuals possessing the most favorable combinations of characters

'Evolution from this point of view," says Morgan,[1] ' has consisted largely in introducing (by mutations) new factors that influence characters already present in the animal or plant

' Such a view gives us a somewhat different picture of evolution from the old idea of a ferocious struggle between the individuals of a species with the survival of the fittest and the annihilation of the less fit Evolution assumes a more peaceful aspect New advantageous characters survive by incorporating themselves into the race improving it and opening to it new opportunities In other words the emphasis may be placed less on the competition between the indi

[1] T H Morgan *A Critique of the Theory of Evolution* (Princeton University Press, 1916) pp 87 88

viduals of a species (because the destruction of the less fit does not *in itself* lead to anything that is new) than on the appearance of new characters and modifications of old characters that become incorporated in the species, for on these depends the evolution of the race'

HYBRIDIZATION AND THE ORIGIN OF SPECIES

As a consequence of the great interest aroused by Mendel s hybridization experiments the question has arisen as to the rôle of hybridization in organic evolution Certain it is that a vast number of animal and plant races now existing are mixed or hybrid in nature and are continually splitting up into various Mendelian segregates How many pure races are there today? Some authors think that no variable races today are pure *Lotsy* goes so far as to claim and attempt to prove that unit characters are fixed and that the only source of variation is hybridization, or amphimixis Biologists today would not be willing to go thus far with *Lotsy* but it seems beyond question that hybridization has played an important rôle in the pro duction of very many groups now living It is of interest to recall that Linnaeus though a special creationist, admitted the possibility of the origin of new species by hybridization

NEO-MENDELIAN DEVELOPMENTS

Since the rediscovery of Mendel s paper by De Vries and its perusal by thousands of biologists the world over, Mendelian breeding experi ments with all manner of animals and plants has been the ruling passion of geneticists Among the leading neo Mendelians are Bate son Morgan Castle, Correns East, Hurst, Shull, Tschermak and the pupils of these

Perhaps the first two mentioned Bateson and Morgan have con tributed most largely to an understanding of the intricacies of the Mendelian operations *Bateson* has become so imbued with the idea that all mutations are the result of the loss of factors that he proposes the hypothesis that ' evolution has taken place through the steady loss of inhibiting factors, as Morgan puts it Living matter was stopped down so to speak, at the beginning of the world As the stops are lost new things emerge Living matter has changed only in that it becomes simpler It is quite probable that Bateson, in proposing so radical a view, intended to be taken only half seriously Apart from this his best known expression of opinion Bateson is the

author of a large amount of fine work in genetics and will rank high in the history of the subject

T H Morgan our leading American geneticist is best known for his researches into the mechanism of Mendelian inheritance Through the statistical study of ratios and linkages of characters in the fruit fly *Drosophila* it has been possible to chart the localities of the determiners or genes of at least 400 mutant characters He has shown that four linked groups of genes exist corresponding to the four kinds of chromosomes of the germ cells one of these groups is sex linked and is therefore to be assigned to the X-chromosome of the mutant male Two other large groups are to be located in the two large autosomes and one very small group is assumed to be located in the microsome Not only have characters or their determiners been assigned to given chromosomes, but they have been located in a linear series on a given chromosome So accurately have these loci been determined that they may be used to predict unknown breeding ratios It would seem that when a theory serves so well that it may be used to predict the results of experiments such a theory must be founded on facts Morgan and his collaborators in genetics are now convinced that they have discovered the actual mechanism of heredity in the behavior of the chromosomes in maturation and fertilization and that it is unexpectedly simple Their views have aroused considerable opposition but they have apparently met successfully all attacks up to the present If it be true that the actual machinery of variation and heredity has been discovered we are farther along in our understanding of the causo-mechanical basis of evolution than we could have hoped to be at so early a date

HEREDITY AND SEX

Since Darwin s theory of sexual selection sex has been a complicating factor in evolutionary theories and one of the chief advances of the present century has been in connection with the factors controlling sex determination and sex differentiation The evolution of sex has also been a subject for considerable research

It now appears that sex is an inherited Mendelian character, the determiner of which is carried in a definite chromosome or group of chromosomes Cytological examination of germ cells under the able leadership of *E B Wilson* has now made it certain that sex, if not directly the result of the presence or absence of specific chromosomes at least is absolutely correlated with such chromosomes It appears however that the sex which is settled by the chromosome

mechanism at the time of fertilization may or may not realize its normal somatic differentiation, depending upon the presence or absence of the proper environment Cases are on record in which an individual germinally determined as a female may be caused to develop the secondary sexual characters of the male or even to produce sperms instead of eggs A great deal of extremely interesting work on sex control and sex reversals has been done within the last half-dozen years and new discoveries are being made almost daily In fact, it might be said that the genetic study of sex marks the high tide level of modern genetic advance

THE EXPERIMENTAL INDUCTION OF HEREDITARY VARIATIONS

With the problem of the mechanism of the heredity of individual differences solved, at least in its more important essentials attention has gradually shifted to the problem as to how individual differences arise They seem to arise suddenly and as though of their own accord and the study of their heredity does not throw much light on the problem of their origin At the present time a massed attack is being made upon the problem of the mode or modes of origin of new hereditary characters The most striking success in the artificial induction of mutations has been obtained by *H F Muller* using as his material the already intensively studied fruit fly *Drosophila melanogaster* By the use of rather heavy doses of X rays he succeeded in increasing the frequency of mutations about 1 500 per cent Nearly all of the mutations produced by this method were the same as those that occur spontaneously but many more occur in a given time

Many other investigators following Muller s methods have succeeded in greatly hastening the pace of mutation in various animals and plants The ability to produce such large numbers of mutants at will furnishes abundant material for genetic investigation and promises greatly to increase our knowledge of the intimate details of the mechanisms of variation and heredity

The most pressing problem of the present is that of discovering how and when genes act during the course of development in producing the characters of the organism Some progress has been made in this direction

THE RECENT ATTACK UPON EVOLUTION IN THE UNITED STATES

The recent highly advertised attack upon the validity of the principle of evolution by certain individuals and religious bodies is hardly to be considered as forming a part of the history of the science,

but it is significant as an influence that may serve either greatly to accelerate or to retard the progress of our science The writer s own experience is that the controversy has greatly enhanced popular interest in this subject, as evidenced by the growing demand for books on evolution and allied subjects and the marked increase in the numbers of students in the colleges who wish to elect courses along these lines

CONCLUDING REMARKS

Now that we have traced the evolution of the science of organic evolution from its crude beginnings among the Greeks up to the present we are in a position to go back and make a systematic study of some of the more important phases of evolutionary science Charles Darwin found it necessary to prove the fact of organic evolution before attempting to discover its causes His method of proof was to marshal a great array of facts which agree with the idea of descent with modification and we shall follow Darwin s method in the subsequent chapters dealing with the evidences of evolution

NOTE —In the first half of the present historical account many short passages are presented in quotation marks without mentioning the source of the quotation In all such cases it will be understood that these passages are from H. F O born s book *From the Greeks to Darwin* (The Macmillan Company)

PART II

EVIDENCES OF ORGANIC EVOLUTION

CHAPTER III

IS ORGANIC EVOLUTION AN ESTABLISHED PRINCIPLE?

1 Is there definite proof of organic evolution?

2 If so what is the nature of the proof?

3 What are the evidences of evolution and in what ways do these bear witness that evolution has occurred and is still occurring?

Before presenting in any detail the several bodies of data that constitute the evidences of evolution let us anticipate a little by attempting to answer the three questions just propounded

1 Reluctant as he may be to admit it honesty compels the evolutionist to admit that there is no absolute proof of organic evolution But, for that matter there is no absolute proof of any thing that depends on records of past events We have no absolute proof that Caesar or Napoleon once lived or fought or conquered All we have are the accounts left by the historians which we accept without question because they are the products of human thought and imagination There is no absolute proof for either of the more or less directly opposed theories of the origin of the material universe the nebular hypothesis of Laplace and the planetesimal hypothesis of Chamberlin and Moulton Both of these theories rest upon exactly the same types of evidences as does the theory of organic evolution viz, the amassing of facts which appear to be explicable on the assumption that the one or the other theory is true If all of the facts are in accord with it and none are found that are incapable of being reconciled with it a working hypothesis is said to have been advanced to the rank of a proved theory As yet it is impossible to say that either of these theories as to the origin of the universe has been proved Yet there is much less popular opposition to the acceptance of these theories as facts than there is to the general theory of organic evolution Similarly, there are certain widely accepted theories of the origin of the present conditions of the earth s crust and its liquid and gaseous envelopes The accepted theory as given us by Hutton and especially by Lyell is essentially an evolutionary theory and depends for its proof on almost exactly the same types of evidence as does that

of organic evolution The basis of the accepted theory of geological evolution is the uniformitarian doctrine of Lyell, which assumes that the key to the past lies in the present, that the changes that are going on today are of the same order and kind as those of the past, and finally that there is neither beginning nor end to the earth's evolutionary history but that a slow and orderly development has gone on and will continue indefinitely The proof of this conception consists of an array of facts derived from a study of the earth's crust including its stratified structure of traces of animal and plant life preserved in the rocks of observed changes in continental contours going on today of erosion going on in coasts and streams, and of a considerable array of facts derived from a study of other worlds than ours in the making The theory of geologic evolution meets with scarcely any opposition today although its foundations are no more securely based than are those of organic evolution

In a sense the proofs of the atomic ionic and electron theories are even less absolutely established than is that of organic evolution, because no one has ever seen nor ever can see an atom an ion, or an electron Chemical and physical facts are rationalized by assuming the existence of these units with their various properties The only evidences of the existence of atoms ions and electrons appear in the facts that on the assumption that they exist, the whole array of observed chemical and physical phenomena are rationalized and bound together into a coherent consistent, and intelligible system In other words with the atomic ionic, and electron theories chemistry and physics are highly rational sciences without these theories the phenomena of physics and chemistry would be a hopeless hodgepodge Yet who would say that these fundamental theories are absolutely proved?

The only type of proof of phenomena that cannot be directly observed or that pertain to the remote past is *circumstantial* proof By analogy we conclude that certain changes took place thus and so in the past because we observe similar changes going on today Every past event has left a trace and it is the task of the historian, antiquarian, or evolutionist to discover and to interpret these traces Sometimes the traces exist as vestiges in modern life and are meaningless unless related to their origin in the past The task of the student of organic evolution is to gather all of the traces of past changes both in living creatures today and in the preserved remains of creatures of the remote past A collection of traces of evolution involves many

apparently unrelated bodies of phenomena There are evidences of evolution in the grouping of animals into phyla classes orders families genera species varieties and races in the homologies that exist in general structure and in particular organs between different *groups of animals and plants in the orderly process of ontogeny* or embryonic development of the individual in actual blood relationship, based upon chemical reactions on the succession of extinct animals and plants found as fossils imbedded in the geologic strata in the present geographical distribution of the various groups of animals and plants in the light of data derived from a study of geological changes, and finally in experimental evolution which involves the observation under experimental control of changes in organisms and the origin of new varieties or elementary species

2 The nature of the proof of organic evolution then is this that using the concept of organic evolution as a working hypothesis it has been possible to rationalize and render intelligible a vast array *of observed phenomena the real facts upon which evolution rests* Thus *classification (taxonomy) comparative anatomy embryology* palaeontology zoogeography and phytogeography serology genetics become consistent and orderly sciences when based upon evolutionary foundations and when viewed in any other way they are thrown into the utmost confusion There is no other generalization known to man which is of the least value in giving these bodies of fact any sort of scientific coherence and unity In other words the working hypothesis works and is therefore acceptable as truth until overthrown by a more workable hypothesis Not only does the hypothesis work but with the steady accumulation of further facts the weight of evidence is now so great that it overcomes all intelligent opposition by its sheer mass There are no rival hypotheses except the outworn and completely refuted idea of special creation now retained only by the ignorant the dogmatic and the prejudiced

3 In answer to the question What are the evidences of evolution and in what ways do these bear witness that evolution has occurred and is still occurring? ' we may present an ordered list of subjects that are to be taken up serially in detail In connection with each of these bodies of evidence the character of their witness-bearing will be discussed

Some of the evidences are more direct and freer from purely interpretative construction than others Some evidences are primary and foundational some are in themselves rather inconclusive but serve

to confirm other facts, and, when reinforced by other evidences, are themselves strongly substantiated Perhaps the crowning evidence of the truth of evolution is that all of these diverse bodies or phenomena invariably support one another and all point in the same direction and to the same conclusion, viz, that organic evolution is a fact

In the former edition of this book the evidences of evolution were presented in a somewhat arbitrary order the evidences that seemed to furnish the most direct proof being, for pedagogical reasons presented first and the more controversial evidences last Experience, however, has shown that for an appreciation of the data from paleontology and from geographic distribution the student must have a knowledge of the principles of morphology (comparative anatomy) and of classification We have therefore changed the order of presentation of the evidences to one that has the authority of precedent The order of treatment will be as follows

I *The fundamental assumption underlying all the evidences*

II *Comparative anatomy (homologies and vestigial structures)* the evidence of the fact that structures in unlike organisms have a common plan and mode of origin that changes have occurred that are in some way related to changes in habit or environment

III *Classification* the evidence that the present groups of animals and plants have arisen by descent with modification '

IV *Serology (blood precipitation tests)* the evidence that the chemical specificity of the blood parallels taxonomic specificity

V *Embryology (the doctrine of recapitulation)* the evidences that the embryonic development of the individual follows the main outlines of the evolutionary history of its ancestors

VI *Paleontology* the evidences afforded by a study of the distribution in time (vertical distribution in the earth s strata) of the fossil remains of extinct animals and plants

VII *Geographic distribution* the evidences afforded by present (also to some extent past) horizontal distribution of contemporaneous animals and plants

VIII *Genetics (experimental evolution)* evidences that heritable variations have occurred under observation in large numbers and in many species of animals and plants and that new varieties of animals and plants have been produced by processes known to man and to a large extent controlled by him

CHAPTER IV

THE FUNDAMENTAL POSTULATE UNDERLYING ALL EVIDENCES OF EVOLUTION

Every science rests in last analysis upon certain postulates or justifiable assumptions, certain verified or verifiable truths that must be admitted before any progress can be made in gaining a further understanding of the content of that science Geology for example must assume as valid the dynamical laws of Newton and the law of gravitation as well as basic laws of chemistry Biology assumes the validity of the laws of physics and chemistry for biology is the fundamental science of the transformations of matter and of energy in living matter but in addition there are also some biological postulates that seem to be so well established that they have come to be thought of as truisms

One of the truisms of biology is the familiar fact that like produces like How surprised one would be if sparrows had anything but sparrows for offspring or if two Caucasic parents were to have a Negro child! Now, a careful survey of the situation reveals the fact that the only postulate the evolutionist needs is no more nor less than a logical extension of what the layman considers a truism or a self evident fact namely, that fundamental structural resemblance signifies genetic relationship that generally speaking *the degree of closeness of structural resemblance runs essentially parallel with closeness of kinship* Most biologists would say that this is not merely a postulate but one of the best established laws of life However obvious the validity of this postulate may be it is the plain duty of one who attempts to justify the evolutionary principle to avoid taking any steps that are open to the least bit of valid criticism If we cannot rely upon this postulate which may be called the principle of homology we can make no sure progress in any attempt to establish the validity of the principle of evolution

The postulate we are now discussing is tantamount to an affirmation of the fact of *heredity* We rely upon this fact in our everyday life When we plant a certain kind of seed we expect to get a certain kind of plant when we breed a certain kind of dog we expect offspring

of the same breed It would be a freak of nature were we to discover any marked exception to the laws of heredity Furthermore our ordinary daily contact with other members of our own species have taught us that as a rule the more closely alike people are the more closely are they related We recognize that children of the same family are more alike in their personal characteristics than are members of the same race not so closely related Whenever we see two people whose resemblance is very great we assume a relatively close kinship Thus everyone has had the experience of meeting two people so strikingly alike that it is almost impossible to distinguish them apart and of immediately assuming that such persons are identical or duplicate twins Now the interesting thing about such twins is that they are vastly more closely related than are ordinary brothers and sisters or even than are fraternal twins who are only brothers and sisters that happen to have been conceived and born simultaneously as the result of the fertilization of two egg cells For duplicate twins are the products of the early division into two equivalent parts of a single embryo derived from one fertilized egg No closer kinship can well be imagined than this for the two individuals bear the same relationship to each other as do the bilateral halves of one individual.

The writer has had an exceptional opportunity of determining the exact degree of resemblance existing between separate offspring derived from a single egg It so happens that a peculiar species of mammal the nine banded armadillo of Texas always gives birth to four young at a time These quadruplets are invariably all of the same sex in a litter and are nearly identical even in their finest anatomical details such as the numbers and arrangements of the plates and scales in the armor and the numbers of hairs in a given area of the skin. A detailed study of the embryonic history of this species has proved beyond any question that in every case the four young in a litter result from a very early division of a single embryo derived from a single fertilized egg (see Fig 52) Large numbers of sets of quadruplets were studied statistically to determine the exact degree of their resemblance to one another A comparison of over two hundred sets revealed the somewhat startling fact that on the average they were over 93 per cent identical (more technically they showed a coefficient of correlation of over 93) The remarkable closeness of this degree of resemblance may be fully appreciated when it is realized that the only structural resemblance belonging to this order of closeness is that existing between the right and left antimeric halves of a single indi

vidual, such as the right and left sides of your own face or your two hands and that the next degree of closeness of resemblance is that between siblings (brothers and sisters) who are only 50 per cent identical (having a coefficient of correlation of only 5) while cousins of various grades have proportionately lower and lower degrees of resemblance in exact ratio with their grades of kinship

This, then is a crucial test of the validity of the postulate that closeness of resemblance is in proportion to closeness of kinship for we have in identical twins and in armadillo quadruplets the closest resemblance associated with the closest possible genetic relationship and we also see that there is an exact proportion between all other known grades of kinship and their relative degree of resemblance

Employing the principle of homology in a somewhat broader way and in a way that is hardly likely to be questioned even by the most captious we account for the common possession of certain structural peculiarities by all members of a given kind or species of animal or plant by saying that such characters have been derived from a common ancestor It is only a short step in logic to conclude that two similar kinds or species of animal have been derived one from the other or both from a common ancestral species Once having taken this step we are on the road that leads inevitably to an evolutionary interpretation of natural groups If the principle of heredity holds for siblings (offspring of the same parents) for races for species where are we to draw the line? It does not seem reasonable to admit that structural resemblances between siblings between races between species are accounted for as the product of heredity and to deny that equally plain resemblances of essentially the same sort among the species of a genus or among the genera of a family have a similar hereditary basis It is logically impossible to draw the line at any level of organic classification and say that structural resemblance is the product of heredity up to such and such a level but that beyond this arbitrarily chosen point heredity ceases to operate

The principle of heredity and its necessary implications constitute the only postulate that is necessary for the evolutionist to make in order to go ahead on a sound basis with a presentation of the evidences of evolution Give him this one point and he asks no further concessions And this is not so much of a concession as it might seem at first blush for the special creationist assumes more potency for heredity than does the evolutionist since he believes in descent without modification a sort of stereotyped heredity slavishly duplicating

forever a fixed set of structural patterns without variation or improvement Since then both special creationist and evolutionist find it equally necessary to assume the principle of heredity there should be little argument on this score But let the reader beware at this point in the discussion for if he admits the postulates already presented—and how can he help but admit them?—he cannot avoid the inevitable conclusion that the theory of descent with modification is the only reasonable explanation of organic resemblances and differences

HOMOLOGY VERSUS ANALOGY

Much difficulty in connection with the study of resemblances and differences in animal and plants is occasioned by a failure to understand the fact that there are two kinds of resemblances and differences Structures that are similar in anatomical detail and in their mode of embryonic origin irrespective of whether they perform the same or different functions are known as *homologous* The test of homological equivalence is a study of the anatomical details of the adult structure followed by a study of the developmental history of the part in question If the part under examination be a bone for example this bone must have a certain relation to the other bones must occur in a certain part of the body must be supplied with certain muscle attachments, in order to be considered homologous with another bone that has the same relations If two structures have the same anatomical relations and arise from equivalent embryonic rudiments they are said to be homologous in spite of small or great differences in relative size appearance or function If structures are homologous it is believed that they represent the same hereditary units and that these equivalent hereditary units have been derived from the same or similar ancestors

Analogous structures are of an entirely different sort They may be more or less superficially alike in form or in function usually in both though anatomically quite different As an example of analogous structures let us examine the three types of aquatic vertebrates shown in Figure 80 These three kinds of vertebrates one a fish one a reptile and the third a mammal might be mistaken by the casual observer to be all fishes of different kinds All have the same fusiform body with lines best adapted for swift locomotion in the water all have median paired and caudal fins all swim in about the same way Yet the resemblance is only skin deep as it were for beneath the surface the one is all fish the second all reptile and the third all mammal The structures that look alike and function alike are from the stand

point of anatomical relations and embryonic derivation entirely different. The resemblances which are so obviously superficially are examples of *analogy*, not of homology, and are the result of molding unlike materials into a semblance of likeness in adaptation to a common environment. Analogous structures while not considered as evidences of kinship are strong evidences of descent with modification, for their very existence implies that they have been changed from a former condition to one in which they are adapted to a new medium To illustrate this point, call to mind that both the ichythyosaur and the porpoise (Fig 80, *B* and *C*) belong to groups that are fundamentally terrestrial air breathing vertebrates, and that whatever they have that is fishlike must be interpreted as adaptive modifications for aquatic life This type of conception and the way in which it bears witness for organic evolution is well brought out in the next chapter by George John Romanes a chapter that for a generation has been considered a classic. A few of the statements in this chapter would in all probability, be somewhat altered if the author were to rewrite it in the light of newer knowledge but on the whole the statements made would still have the support of the most critical of modern anatomists.

CHAPTER V

EVIDENCES FROM MORPHOLOGY (COMPARATIVE ANATOMY)[1]

GEORGE JOHN ROMANES

The theory of evolution supposes that hereditary characters admit of being slowly modified wherever their modification will render an organism better suited to a change in its conditions of life. Let us then observe the evidence which we have of such adaptive modifications of structure in cases where the need of such modification is apparent. We may begin by again taking the case of the whales and porpoises. The theory of evolution infers, from the whole structure of these animals, that their progenitors must have been terrestrial quadrupeds of some kind, which gradually became more and more aquatic in their habits. Now the change in the conditions of their life thus brought about would have rendered desirable great modifications of structure. These changes would have begun by affecting the least typical—that is, the least strongly inherited—structures, such as the skin, claws and teeth. But as time went on, the adaptations would have extended to more typical structures, until the shape of the body would have become affected by the bones and muscles required for terrestrial locomotion becoming better adapted for aquatic locomotion, and the whole outline of the animal more fish like in shape. This is the stage which we actually observe in the seals, where the hind legs, although retaining all their typical bones, have become shortened up almost to rudiments, and directed backwards, so as to be of no use for walking while serving to complete the fish like taper of the body (Fig. 1). But in the whales the modification has gone further than this so that the hind legs have ceased to be apparent externally, and are only represented internally—and even this only in some species—by remnants so rudimentary that it is difficult to make out with certainty the homologies of the bones; moreover, the head and the whole body have become completely fish like in shape (Fig. 2). But profound as are these alterations, they affect only

[1] From G. J. Romanes, *Darwin and after Darwin* (copyright 1892). Used by special permission of the publishers, The Open Court Publishing Company.

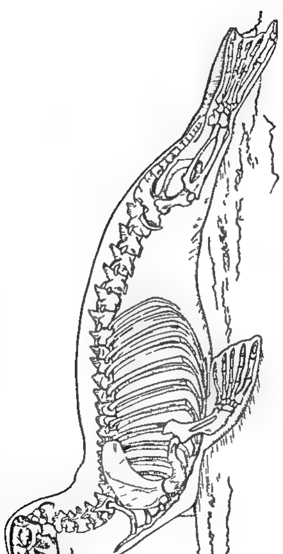


FIG 1—Skeleton of seal $\frac{1}{8}$ nat size (*From Romanes*)

those parts of the organism which it was for the benefit of the organism to have altered so that it might be adapted to an aquatic mode of existence Thus the arm which is used as a fin still retains the bones of the shoulder fore arm wrist and fingers although they are all enclosed in a fin shaped sack so as to render them useless for any purpose other than swimming (Fig 3) Similarly, the head although it so closely resembles the head of a fish in shape still retains the bones of the mammalian skull in their proper anatomical relations to one another but modified in form so as to offer the least possible resistance to the water In short it may be said that all the modifications have been effected with the least possible divergence from the typical mammalian type which is compatible with securing so perfect an adaptation to a purely aquatic mode of life

Now I have chosen the case of the whale and porpoise group because they offer so extreme an example of profound modification of structure in adaptation to changed conditions of life But the same thing may be seen in hundreds and hundreds of other cases For instance to confine our attention to the arm not only is the limb modified in the whale for swimming but in another mammal—the bat—it is modified for flying by having the fingers enormously elongated and overspread with a membranous web

In birds again the arm is modified for flight in a wholly different way—the fingers here being very short and all run together while the chief expanse of the wing is composed of the shoulder and forearm In frogs and lizards again we find hands more like our own but in an extinct species of flying reptile the modification was extreme the wing having been formed by a prodigious elongation of the fifth finger and a membrane spread over it and the rest of the hand (Fig 4) Lastly in serpents the hand and arm have disappeared altogether

Thus even if we confine our attention to a single organ how wonderful are the modifications which it is seen to undergo although never losing its typical character Everywhere we find the distinction between homology and analogy which was explained in the last chapter—the distinction that is between correspondence of structure and correspondence of function On the one hand we meet with structures which are perfectly homologous and yet in no way analogous the structural elements remain but are profoundly modified so as to perform wholly different functions On the other hand we meet with structures which are perfectly analogous and yet in no way homologous totally different structures are modified

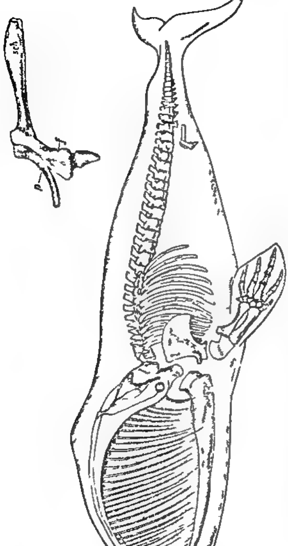


FIG 2.—Skeleton of Greenland whale 1/100 nat size The rudimentary bones of the pelvis are shown on a large scale in the upper drawing (From Romanes after Flower)

to perform the same functions How then are we to explain these things? By design manifested in special creation or by descent with adaptive modification? If it is said by design manifested in special creation we must suppose that the Deity formed an archetypal plan of certain structures and that he determined to adhere to this plan through all the modifications which those structures exhibit But, if so why is it that some structures are selected as typical and not others? Why should the vertebral skeleton for instance be tortured

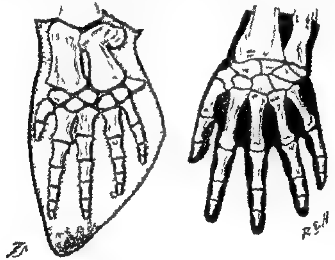


FIG 3—Paddle of whale compared with hand of man (*From Romanes*)

into every conceivable variety of modification in order to subserve as great a variety of functions while another structure such as the eye is made in different sub kingdoms on fundamentally different plans notwithstanding that it has throughout to perform the same function? Will any one have the hardihood to assert that in the case of the skeleton the Deity has endeavored to show his ingenuity, by the manifold functions to which he has made the same structure subservient while in the case of the eye he has endeavored to show his resources by the manifold structures which he has adapted to serve the same function? If so it becomes a most unfortunate circumstance that throughout both the vegetable and animal kingdoms all cases which can be pointed to as showing ingenious adaptation of the

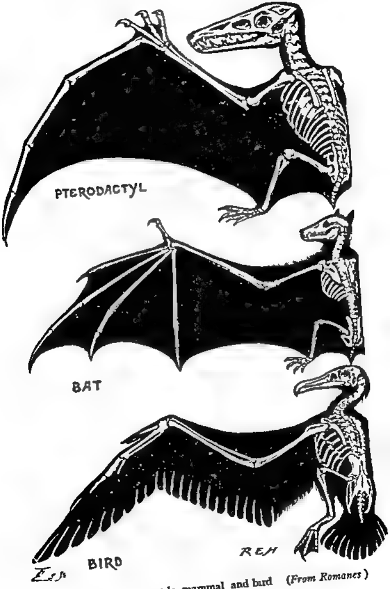


FIG 4—Wing of reptile mammal and bird (*From Romanes*)

same typical structure to the performance of widely different functions—or cases of homology without analogy—are cases which come within the limits of the same natural group of plants and animals and therefore admit of being equally well explained by descent from a common ancestry, while all cases of widely different structures performing the same function—or cases of analogy without homology are to be found in different groups of plants or animals, and are therefore suggestive of independent variations arising in the different lines of hereditary descent

To take a specific illustration The octopus, or devil fish belongs to a widely different class of animals from a true fish and yet its eye in general appearance looks wonderfully like the eye of a true fish Now, Mr Mivart pointed to this fact as a great difficulty in the way of the theory of evolution by natural selection because it must clearly be a most improbable thing that so complicated a structure as the eye of a fish should happen to be arrived at through each of two totally different lines of descent And this difficulty would, indeed be a formidable one to the theory of evolution if the similarity were not only analogical but homological Unfortunately for the objection however Darwin clearly showed in his reply that in no one anatomical or homologous feature do the two structures resemble one another so that in point of fact the two organs do not resemble one another in any particular further than it is necessary that they should, if both are to be analogous or to serve the same function as organs of sight But now suppose that this had not been the case and that the two structures besides presenting the necessary superficial or analogical resemblance, had also presented an anatomical or homologous resemblance with what force might it have then been urged,—your hypothesis of hereditary descent with progressive modification being here excluded by the fact that the animals compared belong to two widely different branches of the tree of life how are we to explain the identity of type manifested by these two complicated organs of vision? The only hypothesis open to us is intelligent adherence to an ideal plan or mechanism But as this cannot now be urged in any comparable case throughout the whole organic world we may on the other hand present it as a most significant fact that while within the limits of the same large branch of the tree of life we constantly find the same typical structures modified so as to perform very different functions we never find any of these particular types of structure in other large branches of the tree That is to say, we never find typical structures

appearing except in cases where their presence may be explained by the hypothesis of hereditary descent ; while in thousands of such cases we find these structures undergoing every conceivable variety of adaptive modification

Consequently, special creationists must fall back upon another position and say,—Well but it may have pleased the Deity to form a certain number of ideal types and never to have allowed the structures occurring in one type to appear in any of the others We answer —Undoubtedly such may have been the case but, if so it is a most unfortunate thing for your theory, because the fact implies that the Deity has planned his types in such a way as to suggest the counter theory of descent For instance it would seem most capricious on the part of the Deity to have made the eyes of an innumerable number of fish on exactly the same ideal type and then to have made the eye of the octopus so exactly like these other eyes in superficial appearance as to deceive so accomplished a naturalist as Mr Mivart and yet to have taken scrupulous care that in no one ideal particular should the one type resemble the other However adopting for the sake of argument this great assumption let us suppose that God did lay down these arbitrary rules for his own guidance in creation and then let us see to what the assumption leads If the Deity formed a certain number of ideal types and determined that on no account should he allow *any part of one type to appear in any part of another* surely we should expect that within the limits of the same type the same typical structures should always be present. Thus remember what efforts so to speak have been made to maintain the uniformity of type in the case of the fore limb as previously explained, and should we not expect that in other and similar cases a similar method should have been followed? Yet we repeatedly find that this is not the case Even in the whale as we have seen the hind limbs are either *altogether absent or dwindled almost to nothing and it is impossible to see* in what respects the hind limbs are of any less ideal value than the fore limbs—which are carefully preserved in all vertebrated animals except the snake and the extinct Dinornis where again we meet in this particular with a sudden and sublime indifference to the maintenance of a typical structure (Fig 5) *Now I say that if the theory* of ideal types is true we have in these facts evidence of a most unreasonable inconsistency But the theory of descent with continued adaptive modification *fully explains all the known cases for in every* case the degree of divergence from the typical structure which an

organism presents corresponds in a general way with the length of time during which the divergence has been going on. Thus we

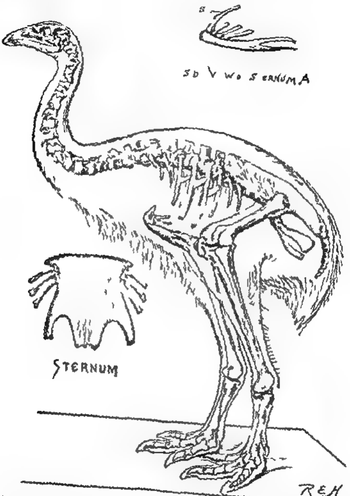


FIG. 5.—Skeleton of *Dinornis gravis* $\frac{1}{8}$ nat. size. Drawn from nature (British Museum). As separate cuts on a larger scale are shown (1) the sternum as this appears in mounted specimens, and (2) the same in profile with its (hypothetical) scapulo coracoid attached. (*From Romanes.*)

scarcely ever meet with any great departure from the typical form with respect to one of the organs without some of the other organs being so far modified as of themselves to indicate on the supposition

of descent with modification that the animal or plant must have been subject to the modifying influences for an enormously long series of generations And this combined testimony of a number of organs in the same organism is what the theory of descent would lead us to expect while the rival theory of design can offer no explanation of the fact, that when one organ shows a conspicuous departure from the supposed ideal type, some of the other organs in the same organism should tend to keep it company by doing likewise

As an illustration both of this and of other points which have been mentioned I may draw attention to what seems to me a particularly suggestive case So-called soldier or hermit-crabs are crabs which have adopted the habit of appropriating the empty shells of mollusks In association with this peculiar habit the structure of these animals differs very greatly from that of all other crabs In particular the hinder part of the body which occupies the mollusk shell and which therefore has ceased to require any hard covering of its own, has been suffered to lose its calcareous integument and presents a soft fleshy character quite unlike that of the most exposed parts of the animal Moreover this soft fleshy part of the creature is especially adapted to the particular requirements of the creature by having its lateral appendages—i e appendages which in other crustacea perform the function of legs— modified so as to act as claspers to the inside of the mollusk shell, while the tail end of the part in question is twisted into the form of a spiral which fits into the spiral of the mollusk shell Now in Keeling Island there is a large kind of crab called *Birgus latro* which lives upon land and there feeds upon cocoa nuts The whole structure of this crab it seems to me unmistakably resembles the structure of a hermit-crab (Fig 6) Yet this crab neither lives in the shell of a mollusk nor is the hinder part of its body in the soft and fleshy condition just described on the contrary it is covered with a hard integument like all the other parts of the animal Consequently I think we may infer that the ancestors of *Birgus* were hermit crabs living in mollusk shells but that their descendants gradually relinquished this habit as they gradually became more and more terrestrial, while concurrently with these changes in habit the originally soft posterior parts acquired a hard protective covering to take the place of that which was formerly supplied by a mollusk shell. So that if so we now have within the limits of a single organism evidence of a whole series of morphological changes in the past history of its species First there must have been the great change from an

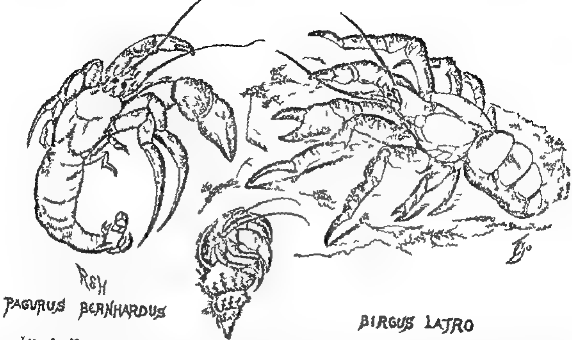


FIG 6—Hermit crabs compared with cocoa nut crab On the left of the illustration one hermit crab is represented as occupying a mollusk shell and another (larger specimen) as it appears when withdrawn from such a shell On the right of the illustration the cocoa nut crab is represented in its natural habitat on land When full grown however it is much larger than our hermit crabs The latter are drawn from life the former from a specimen in the British Museum ½ nat size (*From Romanes*)

ordinary crab to a hermit-crab in all the respects previously pointed out. Next there must have been the change back again from a hermit-crab to an ordinary crab so far as living without the necessity of a mollusk shell is concerned. From an evolutionary point of view therefore we appear to have in the existing structure of *Birgus* a morphological record of all these changes, and one which gives us a reasonable explanation of why the animal presents the extraordinary appearance which it does. But, on the theory of special creation it is inexplicable why this land-crab should have been formed on the pattern of a hermit-crab when it never has need to enter the shell of a mollusk. In other words its peculiar structure is not especially in keeping with its present habits although so curiously allied to the similar structure of certain other crabs of totally different habits in relation to which the peculiarities are of plain and obvious significance.

I will devote the remainder of this chapter to considering another branch of the argument from morphology to which the case of *Birgus* serves as a suitable introduction. I mean the argument from rudimentary structures.

Throughout both the animal and vegetable kingdoms we constantly meet with dwarfed and useless representatives of organs which in other and allied kinds of animals and plants are of large size and functional utility. Thus for instance the unborn whale has rudimentary teeth, which are never destined to cut the gums and throughout its life this animal retains in a similarly rudimentary condition, a number of organs which never could have been of use to any kind of creature save a terrestrial quadruped. The whole anatomy of its internal ear for example has reference to hearing in air, as Hunter long ago remarked 'is constructed upon the same principle as in the quadruped', yet as Owen says the outer opening and passage leading therefrom to the tympanum can rarely be affected by sonorous vibrations of the atmosphere and indeed they are reduced or have degenerated to a degree which makes it difficult to conceive how such vibrations can be propagated to the ear drum during the brief moments in which the opening may be raised above the water.

Now rudimentary organs of this kind are of such frequent occurrence, that almost every species presents one or more of them—usually, indeed, a considerable number. How then, are they to be accounted for? Of course the theory of descent with adaptive modification has a simple answer to supply—namely that when from

changed conditions of life an organ which was previously useful becomes useless it will be suffered to dwindle away in successive generations under the influence of certain natural causes which we shall have to consider in future chapters On the other hand the theory of special creation can only maintain that these rudiments are formed for the sake of adhering to an ideal type Now here again the former theory appears to be triumphant over the latter for without waiting to dispute the wisdom of making dwarfed and useless structures merely for the whimsical motive assigned surely if such a

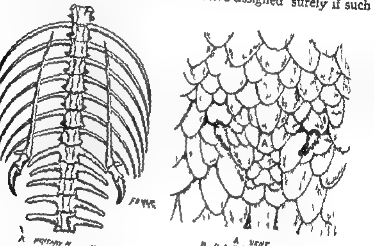


FIG 7 —Rudimentary or vestigial hind limbs of python as exhibited in the skeleton and on the external surface of the animal Drawn from nature ½ nat size (From Romanes)

method were adopted in so many cases we should expect that in consistency it would be adopted in all cases This reasonable expectation, however is far from being realized We have already seen that in numberless cases such as that of the fore limbs of serpents no vestige of a rudiment is present But the vacillating policy in the matter of rudiments does not end here for it is shown in a still more aggravated form where within the limits of the same natural groups of organisms a rudiment is sometimes present and sometimes absent For instance although in nearly all the numerous species of snakes there are no vestiges of limbs in the Python we find very tiny rudiments of the hind limbs (Fig 7) Now is it a worthy conception of Deity that while neglecting to maintain his unity of ideal in the case of

nearly all the numerous species of snakes he should have added a tiny rudiment in the case of the Python—and even in that case should have maintained his ideal very inefficiently inasmuch as only two limbs instead of four, are represented? How much more reasonable is the naturalistic interpretation for here the very irregularity of their appearance in different species, which constitutes rudimentary structures *one of the crowning difficulties to the theory of special* design furnishes the best possible evidence in favour of hereditary

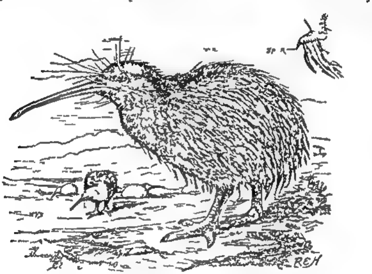


FIG 8—*Apteryx australis* Drawn from life in the Zoological Gardens $\frac{1}{4}$ nat size The external wing is drawn to a scale in the upper part of the cut The surroundings are supplied from the most recent descriptions (*From Romanes*)

descent, seeing that this irregularity then becomes what may be termed the anticipated expression of progressive dwindling due to inutility Thus for example to return to the case of wings we have already seen that in an extinct genus of bird *Dinornis* these organs were reduced to such an extent as to leave it still doubtful whether so much as the tiny rudiment hypothetically supplied to Figure 5 was present in all the species And here is another well known case of another genus of still existing bird which as was the case with *Dinornis*, occurs only in New Zealand (Fig 8) Upon this island there are no four footed enemies—either existing or extinct—to escape from which the wings of birds would be of any service Conse

limestone caverns under nearly the same climate in the two continents of America and Europe so that in accordance with the theory of special creation very close similarity in the organizations of the two sets of faunas might have been expected But instead of this the affinities of these two sets of faunas are with those of their respective continents—as of course they ought to be on the theory of evolution Again what would have been the sense of creating the useless foot stalks for the imaginary support of absent eyes not to mention all the other various grades of degeneration in other cases? So that upon the whole if we agree with the late Professor Agassiz in regarding these cave animals as furnishing a crucial test between the rival theories of creation and evolution we must further conclude that the whole body of evidence which they now furnish is weighing on the side of evolution

So much then for a few special instances of what Darwin called rudimentary structures but what may be more descriptively designated—in accordance with the theory of descent—obsolescent or vestigial structures It is however of great importance to add that these structures are of such general occurrence throughout both the vegetable and animal kingdoms that as Darwin has observed it is almost impossible to point to a single species which does not present one or more of them In other words it is almost impossible to find a single species which does not in this way bear some record of its own descent from other species and the more closely the structure of any species is examined anatomically the more numerous are such records found to be Thus for example of all organisms that of man has been most minutely investigated by anatomists and therefore I think it will be instructive to conclude this chapter by giving a list of the more noteworthy vestigial structures which are known to occur in the human body I will take only those which are found in adult man reserving for the next chapter those which occur in a transitory manner during earlier periods of his life But even as thus restricted the number of obsolescent structures which we all present in our own person is so remarkable that their combined testimony to our descent from a quadrumanous ancestry appears to me in itself conclusive I mean that even if these structures stood alone or apart from any more general evidences of our family relationships they would be sufficient to prove our parentage Nevertheless it is desirable to remark that of course these special evidences which I am about to detail do not stand alone Not only is there the general analogy

furnished by the general proof of evolution elsewhere, but there is likewise the more special correspondence between the whole of our anatomy and that of our nearest zoological allies. Now the force of this latter consideration is so enormous that no one who has not studied human anatomy can be in a position to appreciate it. For without special study it is impossible to form any adequate idea of the intricacy of structure which is presented by the human form. Yet it is found that this enormously intricate organisation is repeated in all its details in the bodies of the higher apes. There is no bone, muscle, nerve, or vessel of any importance in the one which is not answered to by the other. Hence there are hundreds of thousands of instances of the most detailed correspondence, without there being any instances to the contrary, if we pay due regard to vestigial characters. The entire corporeal structure of man is an exact anatomical copy of that which we find in the ape.

My object, then, here is to limit attention to those features of our corporeal structure which, having become useless on account of our change in attitude and habits, are in the process of becoming obsolete, and therefore occur as mere vestigial records of a former state of things. For example, throughout the vertebrated series, from fish to mammals, there occurs in the inner corner of the eye a semi-transparent eye-lid, which is called the nictitating membrane. The object of this structure is to sweep rapidly, every now and then, over the external surface of the eye, apparently in order to keep the surface clean. But although the membrane occurs in all classes of the sub-kingdom, it is more prevalent in some than in others—e.g., in birds than in mammals. Even, however, where it does not occur of a size and mobility to be of any use, it is usually represented, in animals above fishes, by a functionless rudiment, as here depicted in the case of man (Fig. 9).

Now the organisation of man presents so many vestigial structures, thus referring to various stages of his long ancestral history, that it would be tedious so much as to enumerate them. Therefore I will yet further limit the list of vestigial structures to be given as examples, by not only restricting these to cases which occur in our own organisation, but of them I shall mention only such as refer us to the very last stage of our ancestral history—viz., structures which have become obsolescent since the time when our distinctively human branch of the family tree diverged from that of our immediate forefathers, the Quadrumana.

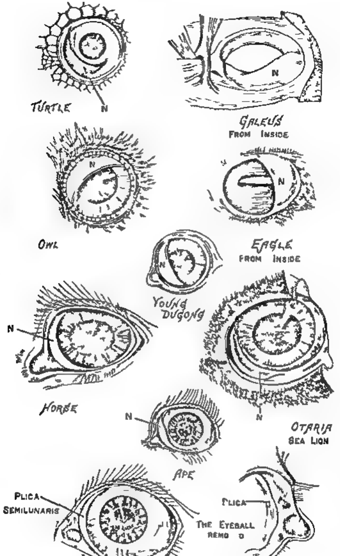


FIG 9—Illustrations of the nictitating membrane in the various animals named drawn from nature The letter N indicates the membrane in each case In man it is called the *pl ca semilunaris* and is represente I in the two lower drawings under this name In the case of the shark (*Galeus*) the muscular membrane i shown as dissected (*From Romanes*)

1 Muscles of the external ear —These which are of large size and functional use in quadrupeds we retain in a dwindled and useless condition (Fig 10) This is likewise the case in anthropoid apes but in not a few other Quadrumana (e g, baboons macacus, magots, etc) degeneration has not proceeded so far and the ears are voluntarily movable

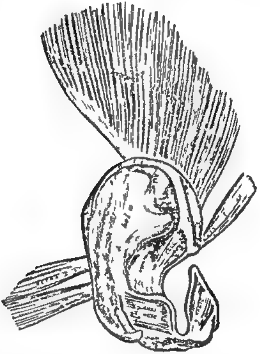


Fig 10 —Rudimentary or vestigial and useless muscles of the human ear (*From Romanes after Gray*)

2 Panniculus carnosis —A large number of the mammalia are able to move their skin by means of subcutaneous muscle as we see, for instance in a horse when thus protecting himself against the sucking of flies We in common with the Quadrumana possess an active remnant of such a muscle in the skin of the forehead, whereby we draw up the eyebrows but we are no longer able to use other considerable remnants of it in the scalp and elsewhere —or more correctly it is rarely that we meet with persons who can But most of the Quadrumana (including the anthropoids) are still able to do so

There are also many other vestigial muscles which occur only in a small percentage of human beings but which when they do occur present unmistakable homologies with normal muscles in some of the Quadrumana and still lower animals

3 Feet —It is observable that in the infant the feet have a strong reflection inwards so that the soles in considerable measure face one another This peculiarity which is even more marked in the embryo than in the infant and which becomes gradually less and

Fig 11 —Portrait of a young gorilla (*From Romanes after Hartmann*)

less conspicuous even before the child begins to walk appears to me a highly suggestive peculiarity For it plainly refers to the condition of things in the Quadrumana seeing that in all these animals the feet are similarly curved inwards to facilitate the grasping of branches And even when walking on the ground apes and monkeys employ to a great extent the outside edges of their feet as does also a child when learning to walk The feet of a young child are also extraordinarily mobile in all directions as are those of apes In order to show these points I here introduce comparative drawings of a young ape and the

lower extremities of a still younger child These drawings moreover, serve at the same time to illustrate two other vestigial characters which have often been previously noticed with regard to the infant's foot I allude to the incurved form of the legs and the lateral extension of the great toe whereby it approaches the thumb like character of this organ in the Quadrumana As in the case of the incurved position of the legs and feet so in this case of the lateral extensibility of the great toe the peculiarity is even more marked in embryonic

FIG 12 —Lower extremities of a young child Drawn from life when the mobile feet were for a short time at rest in a position of extreme inflection (*From Romanes*)

than in infant life For as Professor Wyman has remarked with regard to the foetus when about an inch in length The great toe is shorter than the others and instead of being parallel to them is projected at an angle from the side of the foot thus corresponding with the permanent condition of this part in the Quadrumana So that this organ which according to Owen is perhaps the most characteristic peculiarity of the human structure when traced back to the early stages of its development is found to present a notably less degree of peculiarity

4 Hands —Dr Louis Robinson has recently observed that the grasping power of the whole human hand is so surprisingly great at birth, and during the first few weeks of infancy, as to be far in excess of present requirements on the part of a young child Hence he concludes that it refers us to our quadrumanous ancestry—the young of anthropoid apes being endowed with similar powers of grasping in order to hold on to the hair of the mother when she is using her arms for the purposes of locomotion. This inference appears to me justifiable,

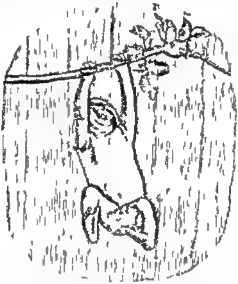


FIG 13 —An infant three weeks old supporting its own weight for over two minutes. The attitude of the lower limbs feet toes is strikingly simian. Reproduced from an instantaneous photograph kindly given for the purpose by Dr L Robinson (*From Romanes*)

inasmuch as no other explanation can be given of the comparatively inordinate muscular force of an infant s grip For experiments showed that very young babies are able to support their own weight by holding on to a horizontal bar, for a period varying from one half to more than two minutes With his kind permission I here reproduce one of Dr Robinson s instantaneous and hitherto unpublished photographs of a very young infant This photograph was taken after the above paragraph (3) was written and I introduce it here because it serves to show incidentally—and perhaps even better than the preceding figure—the points there mentioned with regard

to the feet and great toes Again as Dr Robinson observes the attitude and the disproportionately large development of the arms as compared with the legs give all the photographs a striking resemblance to a picture of the chimpanzee 'Sally at the Zoological Gardens For invariably the thighs are bent nearly at right angles to the body and in no case did the lower limbs hang down and take the attitude of the erect position He adds In many cases no sign of distress is evinced and no cry uttered until the grasp begins to give way

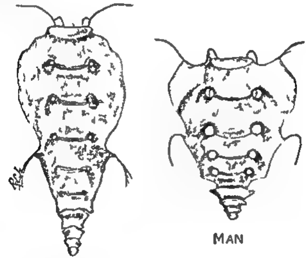


FIG 14 —Sacrum of gorilla compared with that of man showing rudimentary tail bones of each Drawn from nature (*From Romanes*)

5 Tail —The absence of a tail in man is popularly supposed to constitute a difficulty against the doctrine of his quadrumanous descent As a matter of fact however the absence of an external tail in man is precisely what this doctrine would expect seeing that the nearest allies of man in the quadrumanous series are likewise destitute of an external tail Far then from this deficiency in man constituting any difficulty to be accounted for if the case were not so—i e if man did possess an external tail —the difficulty would be to understand how he had managed to retain an organ which had been renounced by his most recent ancestors Nevertheless as the anthro-

poid apes continue to present the rudimentary vestiges of a tail in a few caudal vertebrae below the integuments we might well expect to find a similar state of matters in the case of man And this is just

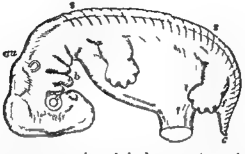


FIG 15 —Diagrammatic outline of the human embryo when about seven weeks old showing the relations of the limbs and tail to the trunk (*After Allen Thompson*) r the radial and u the ulnar border of the hand and forearm t the tibial and f the fibular border of the foot and lower leg au ear s spinal cord u umbilical cord b bronchial gill slits c tail (*From Romanes*)

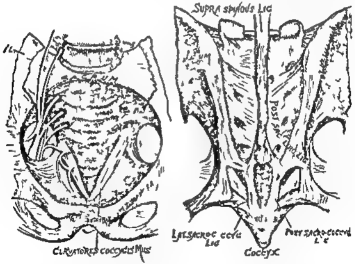


FIG 16 —Front and back view of a lult human sacrum showing abnormal persistence of vestigial tail muscles (*From Romanes*)

what we do find as a glance at these two comparative illustrations will show (Fig 14) Moreover during embryonic life both of the anthropoid apes and of man the tail much more closely resembles

that of the lower kinds of quadrumanous animals from which these higher representatives of the group have descended For at a certain stage of embryonic life the tail both of apes and of human beings is

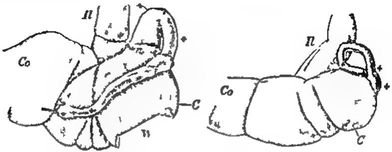


FIG 17 —Appendix vermiformis in orang and in man *Il* ilium *Co* colon *C* coecum *W* a window cut in the wall of the coecum *xxx* the appendix (*From Romanes*)

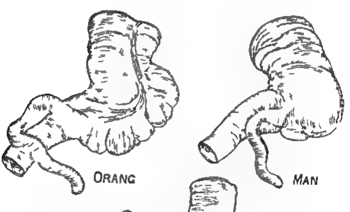


FIG 18 —The same showing variation in the orang (*From Romanes*)

actually longer than the legs (see Fig 15) And at this stage of development also the tail admits of being moved by muscles which later on dwindle away Occasionally however these muscles persist and are then described by anatomists as abnormalities The illustra

tions on page 82 (Fig 16) serve to show the muscles in question, when thus found in adult man

6 **Vermiform appendix of the coecum** —This is of large size and functional use in the process of digestion among many herbivorous animals while in man it is not only too small to serve any such purpose but is even a source of danger to life—many persons dying every year from inflammation set up by the lodgement in this blind tube of fruit stones etc

In the orang it is longer than in man (Fig 17) as it is also in the human foetus proportionally compared with the adult (Fig 18) In some of the lower herbivorous animals it is longer than the entire body

Like the vestigial structures in general however this one is highly variable Thus Figure 18 serves to show that it may sometimes be almost as short in the orang as it normally is in man—both the human subjects of this illustration having been normal

7 **Ear** —Mr Darwin writes

The celebrated sculptor Mr Woolner, informs me of one little peculiarity in the external ear which he has often observed both in men and women The peculiarity consists in a little blunt point, projecting from the inwardly folded margin or helix When present it is developed at birth and according to Professor Ludwig Meyer, more frequently in man than in woman Mr Woolner made an exact model of one such case and sent me the accompanying drawing (Fig 19) The helix obviously consists of the extreme margin of the ear folded inwards and the folding appears to be in some manner connected with the whole external ear being permanently pressed backwards In many monkeys, which do not stand high in the order as baboons and some species of macacus the upper portion of the ear is slightly pointed and the margin is not at all folded inwards but if the margin were to be thus folded a slight point would necessarily project toward the centre In Figure 20 is shown an accurate copy of a photograph of the foetus of an orang (kindly sent me by Dr Nitsche) in which it may be seen how different the pointed outline of the ear is at this period from its adult condition when it bears a close general

FIG 19 —Human ear modeled and drawn by Mr Woolner *a* the projecting point (*From Romanes*)

resemblance to that of man (including even the occasional appearance of the projecting point shown in the preceding woodcut) It is evident that the folding over of the tip of such an ear unless it is changed greatly during its further development, would give rise to a point projecting inwards [1]

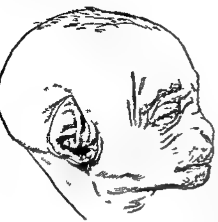


FIG 20 —Foetus of an orang Exact copy of a photograph showing the form of ear at this early stage (*From Romanes*)

The woodcut on page 86 (Fig 21) serves still further to show vestigial resemblances between the human ear and that of apes The last two figures illustrate the general resemblance between the normal ear of foetal man and the ear of an adult orangoutang The other two figures on the lower line are intended to exhibit occasional modifications of the adult human ear which approximate simian characters somewhat more closely than does the normal type It will be observed that in their comparatively small lobes these ears resemble those of all the apes and that while the outer margin of one is not unlike that of the Barbary ape the outer margin of the other follows those of the chimpanzee and orang Of course it would be easy to select individual human ears which present either of these characters in a more pronounced degree but these ears have been chosen as models because they present both characters in conjunction The upper row of figures likewise shows the close similarity of hair tracts and the direction of growth on the part of the hair itself in cases where the *human hair happens to be of an abnormally hirsute character* But this particular instance (which I do not think has been previously noticed) introduces us to the subject of hair and hair growth in general

8 Hair —Adult man presents rudimentary hairs over most parts of the body Wallace has sought to draw a refined distinction between this vestigial coating and the useful coating of quadrumanous animals in the absence of the former from the human back But even

[1] *Descent of Man* (d ed) pp 15–16

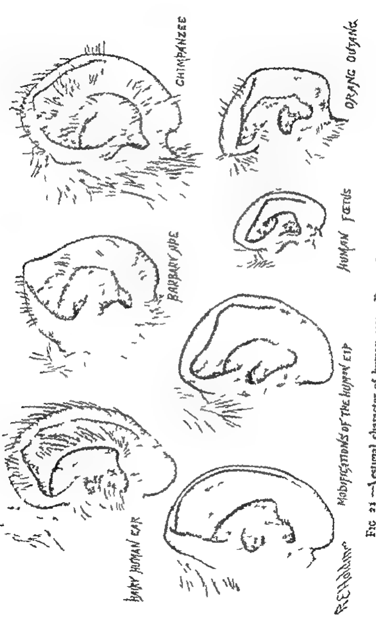


FIG 21 —Vestigial character of human ears Drawn from nature (From Romanes)

this refined distinction does not hold · On the one hand the comparatively hairless chimpanzee which died last year in the Zoological Gardens (*T calvus*) was remarkably denuded over the back and, on the other hand, men who present a considerable development of hair over the rest of their bodies present it also on their backs and shoulders ; Again, in all men the rudimentary hair on the upper and lower arm is directed towards the elbow—a peculiarity which occurs nowhere else in the animal kingdom, with the exception of the anthropoid apes and a few American monkeys, where it presumably has to do with arboreal habits For, when sitting in trees the orang as observed by Mr Wallace, places its hands above its head with its elbows pointing downwards the disposition of hair on the arms and fore arms then has the effect of thatch in turning the rain Again I find that in all species of apes, monkeys, and baboons which I have examined (and they have been numerous) the hair on the backs of the hands and feet is continued as far as the first row of phalanges but becomes scanty or disappears altogether on the second row while it is invariably absent on the terminal row I also find that the same peculiarity occurs in man We all have rudimentary hair on the first row of phalanges, both of hands and feet when present at all it is more scanty on the second row and in no case have I been able to find any on the terminal row In all cases these peculiarities are congenital, and the total absence or partial presence of hair on the second phalanges is constant in different species of Quadrumana For instance it is entirely absent in all the chimpanzees which I have examined while scantily present in all the orangs As in man it occurs in a patch midway between the joints

Besides showing these two features with regard to disposition of hair on the human arm and hand the woodcut on page 88 (Fig 22) illustrates a third By looking closely at the arm of the very hairy man from whom the drawing was taken it could be seen that there was a strong tendency towards a whorled arrangement of the hairs on the backs of the wrists This is likewise as a general rule a marked feature in the arrangement of hair on the same places in the gorilla orang and chimpanzee In the specimen of the latter however from which the drawing was taken this characteristic was not well marked The downward direction of the hair on the backs of the hands is exactly the same in man as it is in all the anthropoid apes Again with regard to hair Darwin notices that occasionally there appears in man a few hairs in the eye brows much longer than the others and that they seem to be

Fig 22 —Hair tracts on the arms and hands of man as compared with those of the chimpanzee Drawn from life (From Romer s)

representative of similarly long and scattered hairs which occur in the chimpanzee, macacus, and baboons

Lastly, it may be here more conveniently observed than in the next chapter on Embryology, that at about the sixth month the human foetus is often thickly coated with somewhat long dark hair over the entire body, except the soles of the feet and palms of the hands, which are likewise bare in all quadrumanous animals This covering which is called the lanugo and sometimes extends even to the whole fore head ears, and face is shed before birth So that it appears to be useless for any purpose other than that of emphatically declaring man a child of the monkey

9 Teeth —Darwin writes

'It appears as if the posterior molar or wisdom teeth were tending to become rudimentary in the more civilized races of man These teeth are rather smaller than the other molars as is likewise the case with the corresponding teeth in the chimpanzee and orang and they have only two separate fangs They are also much more liable to vary both in structure and in the period of their development than the other teeth In the Melanian races on the other hand the wisdom teeth are usually furnished with three separate fangs and are usually sound (i e not specially liable to decay) they also differ from the other molars in size, less than in the Caucasian races

Now in addition to these there are other respects in which the dwindling condition of wisdom teeth is manifested—particularly with regard to the pattern of their crowns Indeed in this respect it would seem that even in the anthropoid apes there is the beginning of a tendency to degeneration of the molar teeth from behind forwards For if we compare the three molars in the lower jaw of the gorilla orang and chimpanzee we find that the gorilla has five well marked cusps on all three of them but that in the orang the cusps are not so pronounced while in the chimpanzee there are only four of them on the third molar Now in man it is only the first of these three teeth which normally presents five cusps both the others presenting only four So that, comparing all these genera together it appears that the number of cusps is being reduced from behind forwards the chimpanzee having lost one of them from the third molar while man has not only lost this but also one from the second molar,—and it may be added likewise partially (or even totally) from the first molar as a frequent variation among civilized races But on the other hand variations are often met with in the opposite direction where the

second or the third molar of man presents five cusps—in the one case following the chimpanzee in the other the gorilla These latter variations therefore may fairly be regarded as reversionary For these facts I am indebted to the kindness of Mr C S Tomes

10 Perforations of the humerus —The peculiarities which we have to notice under this heading are two in number First, the supra condyloid foramen is a normal feature in some of the lower Quadrumana (Fig 24) where it gives passage to the great nerve of

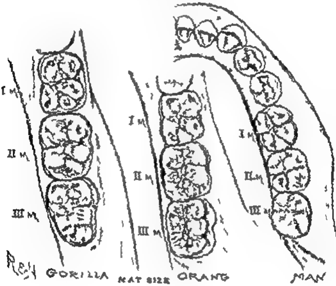


FIG 23 —Molar teeth of lower jaw in gorilla orang and man Drawn from nature nat size (F o n Roman s)

the forearm and often also to the great artery In man however it is not a normal feature Yet it occurs in a small percentage of cases—viz according to Sir W Turner in about one per cent, and therefore is regarded by Darwin as a vestigial character Secondly, there is inter-condyloid foramen which is also situated near the lower end of the humerus but more in the middle of the bone This occurs but not constantly in apes and also in the human species From the fact that it does so much more frequently in the bones of ancient —and also of some savage—races of mankind (viz in 20 to 30 per cent of cases) Darwin is disposed to regard it also as a vestigial feature

On the other hand Prof Flower tells me that in his opinion it is but an expression of impoverished nutrition during the growth of the bone

11 Flattening of Tibia —In some very ancient human skeletons there has also been found a lateral flattening of the tibia, which rarely occurs in any existing human beings but which appears to have been usual among the earliest races of mankind hitherto discovered According to Broca the measurements of these fossil human tibiae resemble those of apes Moreover the bone is bent and strongly

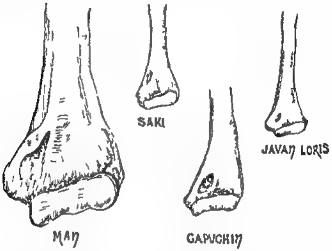


FIG 24.—Perforations of the humerus (supra condyloid foramen) in three species of Quadrumana where it normally occurs and in man where it doe not normally o cur Drawn from nature (*From Romanes*)

convex forwards while its angles are so rounded as to present the nearly oval section seen in apes It is in association with these ape like human tibiae that perforated humeri of man are found in greatest abundance

On the other hand however there is reason to doubt whether this form of tibia in man is really a survival from his quadrumanous ancestry For as Boyd Dawkins and Hartmann have pointed out the degree of flattening presented by some of these ancient human bones is greater than that which occurs in any existing species of anthropoid ape Of course the possibility remains that the unknown species of ape from which man descended may have had its tibia more flattered than is now observable in any of the existing species Never

theless as some doubt attaches to this particular case I do not press it—and indeed only mention it at all in order that the doubt may be expressed

Similarly, I will conclude by remarking that several other instances of the survival of vestigial structures in man have been alleged which are of a still more doubtful character Of such for example, are the supposed absence of the genial tubercle in the case of a very ancient jaw bone of man and the disposition of valves in human veins From the former it was argued that the possessor of this very ancient jaw bone was probably speechless inasmuch as the tubercle in existing man gives attachment to muscles of the tongue From the latter it has been argued that all the valves in the veins of the human body have reference in their disposition to the incidence of blood pressure when the attitude of the body is horizontal or quadrupedal Now the former case has already broken down and I find that the latter does not hold But we can well afford to lose such doubtful and spurious cases in view of all the foregoing unquestionable and genuine cases of vestigial structures which are to be met with even within the limits of our own organization—and even when these limits are still further limited by selecting only those instances which refer to the very latest chapter of our long ancestral history

CHAPTER VI

EVIDENCES FROM CLASSIFICATION

THE PRINCIPLES OF CLASSIFICATION[1]

A F SHULL

The International Code—Some of the essential features of the International Code are as follows The first name proposed for a genus or species prevails on the condition that it was published and accompanied by an adequate description, definition or indication, and that the author has applied the principles of binomial nomenclature This is the so-called *law of priority* The tenth edition of the *Sytema Naturae* of Linnaeus is the basis of the nomenclature The author of a genus or species is the person who first publishes the same in connection with a definition indication or description and his name in full or abbreviated is given with the name thus *Bascanian anthonyi* Stejneger In citations the generic name of an animal is written with a capital letter, the specific and subspecific name without initial capital letter The name of the author follows the specific name (or subspecific name if there is one) without intervening punctuation If a species is transferred to a genus other than the one under which it was first described or if the name of a genus is changed the author s name is included in parentheses For example *Bascanion anthonyi* Stejneger should now be written *Coluber anthonyi* (Stejneger) the generic name of this snake having been changed One species constitutes the *type* of the genus that is it is formally designated as typical of the genus One genus constitutes the type of the subfamily (when a subfamily exists) and one genus forms the type of the family The type is indicated by the describer or if not indicated by him is fixed by another author The name of a subfamily is formed by adding the ending *-inae* and the name of a family by adding *idae* to the root of the name of the type genus For example Colubrinae and Colubridae are the subfamily and family of snakes of which Coluber is the type genus

The basis of classification—Early systematists largely employed superficial characters to differentiate and classify animals and their

[1] From A. F Shull *Principles of Animal Biology* (copyright 1920) Used by special permission of The McGraw Hill Book Company

classifications were thus largely artificial and served principally a convenient methods of arrangement description and cataloging Since the time of the development of the theory of descent with modifications by Lamarck (1809) and Darwin (1859) there has been an attempt to base the classification on relationships Very nearly related animals are put into the same species They are related because they descend from a common ancestry and that common ancestry could not in most cases have been very ancient otherwise evolution within the group would have occurred and the species would have been split into two or more species Species that are much alike are included in one genus being thus marked off from the species of another genus The similarity of the species of a genus is held to indicate kinship but since there is greater diversity among the individuals of a genus than among the members of a species the common stock from which the species of a genus have sprung must have existed at an earlier time in order that evolution could bring about the degree of divergence now observed In like manner a family is made up of genera and their likeness is again a sign of affinity But to account for the greater difference between the extreme individuals belonging to a family evolution must have had more time that is the common source of the members of a family must have antedated the common source of the individuals of a genus Orders classes and phyla are similarly regarded as having sprung from successively more remote ancestors the time differences being necessary to allow for the differences in the amount of evolution This statement is in general correct However since evolution has probably not proceeded at the same rate at all periods nor in all branches of the animal kingdom at any one time the time relations of the groups of high or low rank must not be too rigidly assigned Thus certain genera in which evolution has been slow are probably much older than some families in which evolution has been rapid It is not improbable also that some genera are quite as old as the families which include them but in no case can they be older Furthermore different groups are classified by taxonomists of different temperaments so that groups of a given nominal rank may be much more inclusive (and hence older) in one branch of the animal kingdom than in another On the whole nevertheless the groups of higher rank have sprung from ancestry more remote than that of the groups of lower rank

The means of recognizing the kinship implied in classification permit some differences of opinion It is recognized that likeness in

structural characters is the chief clue to affinities. However, the evidential value of similarity in one or several structures unaccompanied by the similarity of all parts is to be distrusted, since animals widely separated and dissimilar in most characters may have certain other features in common Thus the coots phalaropes and grebes among birds have lobate feet but as indicated by other features they are not closely related, and there are certain lizards (Amphisbaenidae) which closely resemble certain snakes (Typhlopidae) in being blind limbless and having a short tail The early systematists were very liable to bring together in their classification analogous forms that is tho e which are functionally similar or animals which are superficially similar In contrast with the early practice, the aim of taxonomists at the present time is to group forms according to homology, which is considered an indication of actual relationship Since a genetic cla sification must take into consideration the entire animal the search for affinities becomes an attempt to evaluate the results of all morphological knowledge and it is also becoming evident that other things besides structure may throw light upon relationships The fossil records geographical distribution, ecology and experimental breeding may all assist in establishing affinities

The method of taxonomy—It is evident that before the relationships of animals can be determined the forms must be known for unknown forms constitute breaks in the pedigrees of the groups to which they belong Moreover as pointed out above the structural characters variation and distribution must be known before a form can be placed in the proper place in a genetic system For these reasons an important part of systematic work is the de cription of forms and an analysis of their differences After the Linnaean system was adopted zoologists attacked this virgin field and for many years species making predominated Even at the present time when other aspects of zoology have come to receive relatively more attention it is an interesting fact that the analytical method prevails in systematic studies, and taxonomy suffers from and in part merits the criticism that it is a mere cataloging of forms and ignores the higher goal of investigation namely, the discovery of the course of evolution Many systematists however recognize that the ultimate purpose of taxonomic work is to discover the relationships as well as the differences between the described forms in order that the course of evolution may be determined In other words it is appreciated that while analytical studies are necessary they are only preliminary and

that upon their results must be built synthetic studies if taxonomy is to fulfil its purpose

THE METHOD OF CLASSIFICATION

CHARLES DARWIN[1]

Naturalists as we have seen try to arrange the species, genera, and families in each class on what is called the Natural System But what is meant by this system? Some authors look at it merely as a scheme for arranging together those living objects which are most alike and for separating those which are most unlike, or as an artificial method of enunciating, as briefly as possible, general propositions — that is by one sentence to give the characters common for instance to all mammals by another those common to all carnivora by another those common to the dog genus, and then, by adding a single sentence a full description is given of each kind of dog The ingenuity and utility of this system are indisputable But many naturalists think that something more is meant by the Natural System, they believe that it reveals the plan of the Creator but unless it be specified whether order in time or space or both or what else is meant by the plan of the Creator it seems to me that nothing is thus added to our knowledge Expressions such as that famous one by Linnaeus which we often meet with in a more or less concealed form namely, that the characters do not make the genus but that the genus gives the characters, seem to imply that some deeper bond is included in our classifications than mere *resemblance* I believe *that this is the case*, and that community of descent—the one known cause of close similarity in organic beings—is the bond which, though observed by various degrees of modification, is partially revealed to us by our classifications

Let us now consider the rules followed in classification and the difficulties which are encountered on the view that classification either gives some unknown plan of creation or is simply a scheme for enunciating general propositions and of placing together the forms most like each other It might have been thought (and was in ancient times thought) that those parts of the structure which determined the habits of life, and the general place of each being in the economy of nature would be of very high importance in classification Nothing can be more false No one regards the external similarity of a mouse to a shrew, of a dugong to a whale of a whale to a fish as of any

[1] From *The Origin of Species*

importance These resemblances though so intimately connected with the whole life of the being are ranked as merely adaptive or analogical characters but to the consideration of these resemblances we shall recur It may even be given as a general rule that the less any part of the organisation is concerned with special habits the more important it becomes for classification As an instance Owen in speaking of the dugong says The generative organs being those which are most remotely related to the habits and food of an animal I have always regarded as affording very clear indications of its true affinities We are least likely in the modifications of these organs to mistake a merely adaptive for an essential character With plants how remarkable it is that the organs of vegetation on which their nutrition and life depend are of little signification whereas the organs of reproduction with their product the seed and embryo are of paramount importance! So again in formerly discussing certain morphological characters which are not functionally important we have seen that they are often of the highest service in classification This depends on their constancy throughout many allied groups and their constancy chiefly depends on any slight deviations not having been preserved and accumulated by natural selection which acts only on serviceable characters

WHAT IS A SPECIES?

Each kind of animal or plant that is each set of forms which in the changes of the ages has diverged tangibly from its neighbors is called a species There is no absolute definition for the word species The word kind represents it exactly in common language and is just as susceptible to exact definition The scientific idea of species does not differ materially from the popular notion A kind of tree or bird or squirrel is a species Those individuals which agree very closely in structure and function belong to the same species There is no absolute test other than the common judgment of men competent to decide Naturalists recognize certain formal rules as assisting in such a decision A series of fully intergrading forms however varied at the extremes is usually regarded as forming a single species There are certain recognized effects of climate of climatic isolation and of the isolation of domestication These do not usually make it necessary to regard as distinct species the extreme forms of a series concerned

From D S Jordan and V L Kellogg *Evolution and Animal Life*

The term species was thus defined by the celebrated botanist De Candolle 'A species is a collection of all the individuals which resemble each other more than they resemble anything else which can by mutual fecundation produce fertile individuals and which reproduce themselves by generation in such a manner that we may from analogy suppose them all to have sprung from one single individual And the zoologist Swainson gives a somewhat similar definition A species in the usual acceptation of the term is an animal which in a state of nature is distinguished by certain peculiarities of form, size colour or other circumstances from another animal It propagates after its kind individuals perfectly resembling the parent its peculiarities therefore are permanent

As will have become apparent the significant assumption underlying classification is that the closest fundamental similarities between animals (or plants) are found in the forms most closely related and that the greatest differences are found in those forms which are unrelated or at best very distantly related The assumption implies the idea of descent with modification which is no more nor less than evolution Using this evolutionary basis we can arrive at an extremely satisfactory classification both of living and of extinct forms and there is no other basis of classification that works

The question might well be asked whether it is possible to test the validity of the assumption that degrees of resemblance vary directly with closeness of blood relationship? Two direct tests of this may be and have been made The closest of blood relatives possible are individuals that have been derived by the dividing of a single egg Armadillo quadruplets have been shown to be thus derived and detailed studies of the closeness of resemblance existing between members of a given set indicate that they are vastly more alike than are the simultaneously born offspring of animals which give birth to several young, but in which each young is derived from a separate egg If we use the index of correlation to indicate the degree of similarity between individuals we find that ordinary brothers or sisters are only about 50 per cent alike while armadillo quadruplets are over 90 per cent alike Identical or duplicate twins in human beings are believed to have an origin from one egg after the fashion of the armadillo

From A R Wallace *Darwinism*

See H H Newman *The Biology of Twins* (1917) University of Chicago Press

though the proof has not been forthcoming Everyone is familiar with the remarkable similarity amounting almost to identity between such twins Thus we are able to show that the closest blood relationship known is associated with the closest resemblance The next degree of resemblance is between members of the same family brothers sisters, cousins etc. and we do not hesitate to explain this resemblance as due to blood relationship In this we merely accept the known principles of heredity

The second direct test of the validity of the assumption that degrees of resemblance run parallel with degrees of blood relationship is found in connection with blood precipitation tests This evidence, as presented by Professor Scott forms the substance of the next chapter

obtained with the bloods of Simudae (i e, Man like Ape-) closely resemble those obtained with human blood the bloods of Cercopithe cidae (Old World Monkeys) came next followed by those of Cebidae and Hapalidae (New World Monkeys and Marmosets) which gave but slight reactions with anti human serum, whilst the blood of Lemuroidea gave no indication of blood relationship' A perusal of the pages relating to the tests made upon the many bloods I have examined by means of precipitating anti sera will very clearly show that this method of investigation permits of our drawing certain definite conclusions It is a remarkable fact that a common property has persisted in the bloods of certain groups of animals throughout the ages which have elapsed during their evolution from a common ancestor and this in spite of differences of food and habits of life The persistence of the chemical blood relationship between the various groups of animals serves to carry us back into geological times and I believe we have but begun the work along these lines, and that it will lead to valuable results in the study of various problems of evolution

The general conclusions on interrelationships so far as they are of particular interest for our purpose reached by Nuttall and Graham Smith as the result of many thousands of blood tests may be summa rized as follows

1 If sufficiently strong solutions be used and time enough be allowed, a relationship between the bloods of all mammals is made evident

2 The degrees of relationship between man apes and monkeys have already been noted.

3 Anti-carnivore sera show ' a preponderance of large reactions amongst the bloods of Carnivora as distinguished from other Mam malia the maximum reactions usually take place amongst the more closely related forms in the sense of descriptive zoology '

4 Anti pig serum gives maximum reactions only with the bloods of other species of the same family moderate reactions those of rumi nants and camels, and moderate or slight reactions with those of whales Anti llama serum gives a moderate reaction with the blood of the camel and the close relationship between the deer family and the great host of antelopes, sheep goats and oxen is clearly demonstrated

5 Anti whale serum gives maximum reactions only with the bloods of other whales and slight reactions with those of pigs and ruminants.

6 A close relationship is shown to exist between all marsupials with the exception of the *Thylacine, or so-called Tasmanian Wolf*

7 Strong anti turtle serum gives maximum reactions only with the bloods of turtles and crocodiles, with those of lizards and snakes the results are almost negative With the egg albumins of reptiles and birds a moderate reaction is given

8 Anti lizard serum produces maximum results with the bloods of lizards and reacts well with those of snakes

9 These experiments indicate that there is a close relationship between lizards and snakes on the one hand turtles and crocodiles on the other They further indicate that birds are more nearly allied with the turtle crocodile series than with the lizard snake series results for which palaeontological studies had already prepared us

10 "Tests were made by means of anti sera for the fowl and ostrich upon 792 and 649 bloods respectively They demonstrate a similarity in blood constitution of all birds, which was in sharp contrast to what had been observed with mammalian bloods when acted upon by anti mammalian sera Differences in the degree of reaction were observed, but did not permit of drawing any conclusions

11 I have already called attention to the fact that the problematical Horseshoe crab is indicated by its embryology to be related to the air breathing spiders and scorpions rather than to the marine Crustacea It is of exceptional interest to learn that embryology is supported by the results of the blood tests

It must not be supposed that there is any exact mathematical ratio between the degrees of relationship indicated by the blood tests and those which are shown by anatomical and palaeontological evidence Any supposition of the kind would be immediately negatived by the contrast between the blood of mammals and that of birds It could hardly be maintained that an ostrich and a parrot are more nearly allied than a wolf and a hyena and yet that would be the inference from the blood tests Like all other anatomical and physiological characters the chemical composition of the blood is subject to change in the course of evolution and these developmental changes do not keep equal pace in all parts of the organism It is the rule rather than the exception to find that one part of the structure advances much more rapidly than other parts such as the teeth the skull or the feet The human body is fortunately for us of rather a primitive kind while the development of the brain is far superior to that of any other mammal and this great brain development has

necessitated a remodeling of the skull On the other hand, the skeleton, limbs hands and feet are but slightly specialized In the elephant tribe so far as we can trace them back in time, there has been little change, save in size in the structure of the body or limbs while the teeth and skull have passed through a series of remarkable changes It is for this reason that it is unsafe to found a scheme of classification which is meant to be a brief expression of relationship, upon a single character, for the result is almost invariably misleading The results of blood tests must be critically examined and checked by a comparison with the results obtained by other methods of investigation, but after every allowance has been made these tests are very remarkable

The blood tests have brought very strong confirmation to the theory of evolution and from an entirely unexpected quarter they come as near to giving a definite demonstration of the theory as we are likely to find until experimental zoology and botany shall have been improved and perfected far beyond their present state

CHAPTER VIII

EVIDENCES FROM EMBRYOLOGY

THE FACTS OF REPRODUCTION AND DEVELOPMENT

It is now definitely known that all living creatures are mortal, at least as individuals but they all have the capacity of continuing their life by the reproduction of offspring This physical immortality is based upon an actual transmission from parent to offspring of some material substance which is so organized chemically as to be fully representative of the race or stock to which the parent belongs

Reproduction may be *asexual* or *sexual* In *asexual development* a new individual may be produced by a process of *fission* (dividing the parent into two or more parts each of which has the capacity to develop into a whole new individual) by *budding* (the production of new individuals by means of outgrowths of the parent body) or by giving off spores or eggs capable of development without fertilization (*parthenogenesis*) In *sexual reproduction* two kinds of parent individuals exist one a female which is capable of giving off relatively large single cells called eggs (ova) and the other a male which is capable of producing minute usually motile cells called spermatozoa A union of ovum and spermatozoon is usually necessary before the ovum can begin its development It is the sexual method of reproduction that will chiefly concern us here and, for present purposes we may omit any further mention of the various asexual methods

An ovum may be conceived of as an individual of some definite species or race reduced to the very lowest terms It exhibits the characteristic cell structure consisting of cytoplasm and nucleus cell membrane nuclear membrane usually a centrosome (Fig 40) Further details as to the minute structure of the nucleus are given in chapter xliv where the mechanism of Mendelian heredity is dealt with

"The reproductive cells from the two sexes " says Wright,[1] "have very different appearances In mammals the ovum is a relatively large spherical cell, just visible to the naked eye

[1] From Sewall Wright *Principles of Livestock Breeding* United States Department of Agriculture Bulletin No 905

"In birds the yolk of an egg is really a single ovum, distended to an enormous size by food material The sperm cell is very much smaller and can be seen well only with a high power microscope It is something like a tadpole in shape, having a small cell body, containing a little nucleus and attached to this a long whiplike process which beats rapidly while the cell is alive, enabling it to seek out and unite with the large passive egg in the act of fertilization Enormous numbers of sperm cells are produced by the male, but only one takes part in fertilization After the first has penetrated the membrane of an egg cell a change takes place in the latter which prevents the entrance of others

The sperm activates certain formerly inert substances in the egg and the new combination cell (the *zygote*) starts almost at once to produce a new individual

OUTLINE OF ANIMAL DEVELOPMENT[4]

D S JORDAN AND V L KELLOGG

The embryonic development is from the beginning up to a certain point practically alike looked at in its larger aspect for all the many celled animals That is there are certain principal or constant characteristics of the beginning development which are present in the development of all many celled animals The first stage or phenomenon of development is the simple fission of the germ cell into halves (Fig 25 *b*) These two daughter cells next divide so that there are four cells (*c*) each of these divides and this division is repeated until a greater or lesser number (varying with the various species or groups of animals) of cells is produced These cells may not all be of the same size but in many cases they are no structural differentiation whatever being apparent among them

The phenomenon of repeated division of the germ cell is called cleavage and this cleavage is the first stage of development in the case of all many-celled animals The germ or embryo in some animals consists now of a mass of few or many undifferentiated primitive cells lying together and usually forming a sphere (Fig 25 *e*) or perhaps separated and scattered through the food yolk of the egg The next stage of development is this the cleavage cells arrange themselves so as to form a usually hollow sphere or ball, the cells lying side by side to

[4] From D S Jordan and V L Kellogg *Evolution and Animal Life* (copyright 1907) Used by special permission of the publishers D Appleton & Company

form the outer circumferential wall of this hollow sphere (*f*) This is called the *blastula* or *blastoderm* stage of development, and the embryo itself is called the blastula or blastoderm This stage also is common to all the many celled animals The next stage in embryonic development is formed by the bending inward of a part of the blastoderm cell layer, as shown in (*g*) (or the splitting off inwardly of cells from a special part of the blastula cell layer) This bending in may produce a small depression or groove, but whatever the shape or extent of the sunken in part of the blastoderm, it results in distinguishing the blastoderm layer into two parts a sunken in or inner portion called

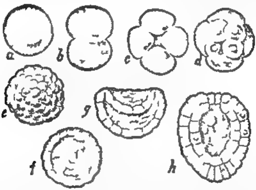


FIG 25 —First stages in the embryonic development of the pond snail *Lymnaeus* *a* egg cell *b* first cleavage *c* second cleavage *d* third cleavage *e* after numerous cleavages *f* blastula—in section *g* gastrula just forming—in section *h* gastrula completed—in section (*From Jordan and Kellogg after Rabl*)

the *endoblast* and the other unmodified portion called the *ectoblast* *Endo* means within and the cells of the endoblast often push so far into the original blastoderm cavity as to come into contact with the cells of the ectoblast and thus obliterate this cavity (*h*) This third well marked stage in the embryonic development is called the *gastrula* stage, and it also occurs in the development of all or nearly all many celled animals

In the case of a few of the simple many celled animals the embryo hatches—that is issues from the egg at the time of or very soon after reaching the gastrula stage In the higher animals however, development goes on within the egg or within the body of the mother until the embryo becomes a complex body composed of many various

tissues and organs. Almost all the development may take place within the egg so that when the young animal hatches there is necessary little more than a rapid growth and increase of size to make it a fully developed mature animal. This is the case with the birds, a chicken just hatched has most of the tissues and organs of a full grown fowl and is simply a little hen. But in the case of other animals the young hatches from the egg before it has reached such an advanced stage of development, a young starfish or young crab or young honeybee just hatched looks very different from its parent. It has yet a great deal of development to undergo before it reaches the structural condition of a fully developed and fully grown starfish or crab or bee. Thus *the development of some animals is almost wholly embryonic development*—that is, development within the egg or in the body of the mother—while the development of other animals is largely postembryonic, or larval development, as it is often called. There is no important difference between embryonic and postembryonic development. The development is continuous from egg cell to mature animal, and whether inside or outside of an egg it goes on regularly and uninterruptedly.

The cells which compose the embryo in the cleavage stage and blastoderm stage and even in the gastrula stage are apparently all similar there is little or no differentiation shown among them. But from the gastrula stage on development includes three important things the gradual differentiation of cells into various kinds to form the various kinds of animal tissues the arrangement and grouping of these cells into organs and body parts and finally the developing of these organs and body parts into the special condition characteristic of the species of animal to which the developing individual belongs. From the primitive undifferentiated cells of the blastoderm, development leads to the special cell types of muscle tissue, of bone tissue of nerve tissue, and from the generalized condition of the embryo in its early stages development leads to the specialized condition of the body of the adult animal. Development is from the general to the special as was said years ago by von Baer the first great student of development.

A starfish, a beetle a dove and a horse are all alike in their beginning—that is the body of each is composed of a single cell a *single structural unit*. And they are all alike or very much alike through several stages of development the body of each is first a single cell then a number of similar undifferentiated cells and then a

blastoderm consisting of a single layer of similar undifferentiated cells But soon in the course of development the embryos begin to differ and as the young animals get further and further along in the course of their development they become more and more different until each finally reaches its fully developed mature form showing all the great structural differences between the starfish and the dove the beetle and the horse That is, all animals begin development apparently alike but gradually diverge from each other during the course of development

There are some extremely interesting and significant things about this divergence to which attention should be given While all animals are apparently alike structurally at the beginning of development so far as we can see they do not all differ noticeably at the time of the first divergence in development The first divergence in development is to be noted between two kinds of animals which belong to different great groups or classes But two animals of different kinds both belonging to some one great group do not show differences until later in their development This can best be understood by an example All the butterflies and beetles and grasshoppers and flies belong to the great group or class of animals called Insecta or insects There are many different kinds of insects and these kinds can be arranged in subordinate groups (orders) such as the Diptera, or flies, the Lepidoptera or butterflies and moths and so on But all have certain structural characteristics in common so that they are comprised in one great class—the Insecta Another great group of animals is known as the Vertebrata or backboned animals The class Vertebrata includes the fishes the batrachians the reptiles the birds and the mammals each composing a subordinate group but all characterized by the possession of a backbone or more accurately speaking of a notochord, a backbonelike structure Now, an insect and a vertebrate diverge very soon in their development from each other but two insects such as a beetle and a honeybee or any two vertebrates such as a frog and a pigeon do not diverge from each other so soon That is all vertebrate animals diverge in one direction from the other great groups but all the members of the great group keep together for some time longer Then the subordinate groups of the Vertebrata such as the fishes the birds and the others, diverge and still later the different kinds of animals in each of these groups diverge from each other

That the course of development of any animal from its beginning to fully developed adult form is—in all its essentials—fixed and certain

is readily seen All rabbits develop in the same way every grasshopper goes through the same developmental changes from single egg cell to the full grown active hopper as every other grasshopper of the same kind—that is development takes place according to certain natural laws the laws of animal development These laws may be roughly stated as follows All many celled animals begin life as a single cell the fertilized egg cell each animal goes through a certain orderly series of developmental changes which, accompanied by growth leads the animal to change from a single cell to the many celled complex form characteristic of the species to which the animal belongs this development is from simple to complex structural condition, the development is the same for all individuals of one species While all animals begin development similarly the course of development in the different groups soon diverges, the divergence being of the nature of a branching like that shown in the growth of a tree In the free tips of the smallest branches we have represented the various species of animals in their fully developed condition all standing more or less clearly apart from each other But in tracing back the development of any kind of animal we soon come to a point where it very much resembles or becomes apparently identical with the development of some other kind of animal and in addition the stages passed through in the developmental course may very much resemble the fully developed mature stages of lower animals To be sure any animal at any stage in its existence differs absolutely from any other kind of animal in that it can develop into only its own kind of animal There is something inherent in each developing animal that gives it an identity of its own Although in its young stages it may be hardly distinguishable from some other kind of animal in similar stages it is sure to come out when fully developed an individual of the same kind a its parents were or are A very young fish and a very young salamander are almost indistinguishably alike but one is sure to develop into a fish and the other into a salamander This certainty of an embryo to become an individual of a certain kind is called the law of heredity Viewed in the light of development there must be as great a difference between one egg and another as between one animal and another for the greater difference is included in the less

The significance of the developmental phenomena is a matter about which naturalists have yet very much to learn It is believed however by practically all naturalists that many of the various stages in the development of an animal correspond to or repeat in ma

fundamental features at least the structural condition of the animal's ancestors. Naturalists believe that all backboned or vertebrate

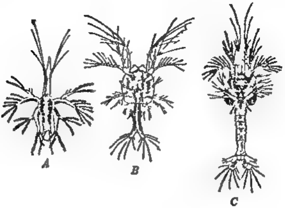


FIG. 26.—Stages in the development of the prawn *Peneus potimirium*. *A* Nauplius larva; *B* first zoea stage; *C* second zoea stage. (*From Jordan and Kellogg after Fritz Müller.*)

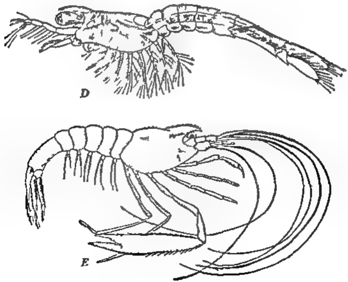


FIG. 27.—Later stages in the development of the prawn *Peneus potimirium*. *D* Mysis stage; *E* adult stage. (*From Jordan and Kellogg.*)

animals are related to each other through being descended from a common ancestor, the first or oldest backboned animal? In fact, it is because all these backboned animals—the fishes, the batrachians, the reptiles, the birds, and the mammals—have descended from a common ancestor that they all have a backbone. It is believed that the descendants of the first backboned animal have in the course of many generations branched off little by little from the original type until there came to exist very real and obvious differences among the backboned animals—differences which among the living backboned animals are familiar to all of us. *The course of development of an individual animal is believed to be a very rapid and evidently much condensed and changed recapitulation of the history which the species or kind of animal to which the developing individual belongs has passed through in the course of its descent through a long series of gradually changing ancestors.* If this is true, then we can readily understand why a fish and a salamander, a tortoise, a bird, and a rabbit, are all much alike, as they really are, in their earlier stages of development, and gradually come to differ more and more as they pass through later and later developmental stages. A crab has a tail in one of its developmental stages, so that at that time it looks like and really is like the mature stage of some tailed crustacean like a crayfish. A barnacle which looks little like a crayfish or crab in its mature stage, is hardly to be distinguished in its immature life from a young crab or lobster. Sacculina, which is a still more degenerate crustacean, is only a sort of feeding sac with rootlet-like processes projecting into the body of the host crab on which it lives as a parasite, but the young free-swimming Sacculina is essentially like a barnacle, crayfish, or crab in its young stage.

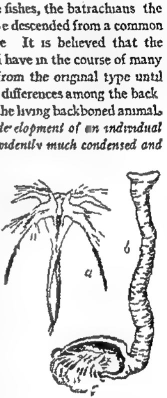


Fig. 28.—Metamorphosis of a barnacle, *Lepas*. *a*, larva; *b*, adult. (*From Jordan and Kellogg.*)

However, it is obvious that this recapitulation or repetition of ancestral stages is never perfect, and it is often so obscured and modified by interpolated adaptive stages and characters that but little of an animal's ancestry can be learned from a scrutiny of its development.

The fascinating biogenetic law of Müller and Haeckel summed up in the phrase, '*ontogeny is a recapitulation of phylogeny*" must not be too heavily leaned on as a support for any speculations as to the phyletic affinities of any species or group of species of organisms ' Embryology is an ancient manuscript with many of the sheets lost others displaced, and with spurious passages interpolated by a later hand "

CHAPTER IX

CRITIQUE OF THE RECAPITULATION THEORY[1]

W B SCOTT

Embryology is the study of the development of the individual organism from its beginning in the egg to the attainment of the adult condition This individual development is called *ontogeny* and the question of the relation of ontogeny to the ancestral history of the species or *phylogeny* constitutes one of the main problems of embryology Around this problem many controversies have raged controversies which have by no means arrived at a definite solution even to-day Thirty years ago the "recapitulation theory" was well nigh universally accepted according to which the individual development, or ontogeny was regarded as an abbreviated repetition of the ancestral history of the species or phylogeny Haeckel called this theory the fundamental biogenetic law and upon it he established his whole History of Creation ' Nowadays that ' fundamental law is very seriously questioned and by some high authorities is altogether denied However even those who take this extreme position concerning the recapitulation theory see in the facts of embryology one of the strongest supports of the doctrine of evolution

It was very early recognized that the recapitulation theory could not be applied with literal exactness, but was subject to certain important exceptions and qualifications

1 That the history must have been enormously abbreviated After three weeks of incubation the tiny speck of protoplasm, which forms a circular mark on the yolk of a hen s egg is developed into a fully formed chick, ready for hatching and able in large degree to take care of itself On the other hand the evolution of birds from their invertebrate ancestors through the fishes amphibians, and reptiles the separation of the gallinaceous stock from other birds and the differentiation of this particular species were extremely slow processes extending through unnumbered millions of years Admitting recapitulation to the fullest extent it is evidently a physical impossibility

[1] From W B Scott *The Theory of Evolution* (copyright 1917) Used by special permission of the publishers, The Macmillan Company

that it should be a perfect repetition of phylogeny, very much of the long story must of necessity be omitted

2 Through all the stages of development the embryo must be rendered able to live and grow and thrive through adaptation to its surroundings and changes in its environment In some animals development takes place within the body of the mother, in others the embryo is protected by the hard egg shell as in birds, while the eggs of certain fishes and many invertebrates float freely in the sea and are almost without protection Such differences in environment necessitate differences in the mode of development while the presence or absence of a large amount of inert food material, or yolk exerts a great influence in determining the steps of ontogeny

3 Many animals pass through a larval stage of development in which the immature young leads an independent and self sustaining existence during which it is very different in appearance and structure from its adult parents Familiar instances of this mode of development are to be found in the tadpole which is the larva of the frog, and the caterpillar, the larva of a butterfly Larvae are fully subject to the struggle for existence and must adapt themselves to their environment and to changes in that environment exactly as do adults if they are to survive In this way many changes are introduced into the ontogeny which can have no phylogenetic significance It is found in several known instances, that nearly allied species living under different conditions, have quite different modes of ontogeny, though their ancestral history must have been substantially identical In one and the same species of marine worms for example which inhabits both the warm Mediterranean and the cold waters of the North Sea the larva of the northern form is quite distinct from that of the southern In attempting to interpret the meaning of embryological facts it is thus necessary to distinguish sharply between those features which are derived from a long inheritance and are therefore called *palingenetic* from those which have been secondarily introduced in response to the changing needs of embryonic or larval life These secondary features are termed *cenogenetic*

'If we are compelled to admit that cenogenetic characters are intermingled with palingenetic, then we cannot regard ontogeny as a pure source of evidence regarding phyletic relationships Ontogeny accordingly becomes a field in which an active imagination has full scope for its dangerous play but in which positive results are by no means everywhere to be obtained To attain such results the palin

genetic and cenogenetic phenomena must be sifted apart, an operation which required more than one critical grain of salt On what grounds shall this critique be based? Assuredly not by way of a vicious circle on the ontogeny again for if cenogenetic characters are present in one case who will guarantee that a second case used for a comparison with the first does not likewise appear in cenogenetic disguise? If it once be admitted that not everything in development is palingenetic, that not every ontogenetic fact can be accepted at its face value, so to speak, it follows that nothing in ontogeny is immediately available for the critique of embryonic development The necessary critique must be drawn from another source

These remarks of Gegenbaur's were called forth by the state of wild speculation into which embryological work had fallen As there were no generally accepted canons of interpretation for the facts of embryological development different writers interpreted these facts in the most divergent and contradictory manner, resulting in a chaotic confusion which led to a strong reaction against the whole method though there can be little doubt that this reaction has gone too far

It must be evident to any candid observer, not only that the embryological method is open to criticism but that the whole fabric of morphology so far as it rests upon embryological evidence, stands in urgent need of reconstruction For twenty years embryological research has been largely dominated by the recapitulation theory, and unquestionably this theory has illuminated many dark places and has solved many a perplexing problem that without its aid might have remained a standing riddle to the pure anatomist But while fully recognizing the real and substantial fruits of that theory, we should not close our eyes to the undeniable fact that it, like many another fruitful theory, has been pushed beyond its legitimate limits It is largely to an overweening confidence in the validity of the embryological evidence that we owe the vast number of the elaborate hypothetical phylogenies which confront the modern student in such bewildering confusion The inquiries of such a student regarding the origin of any of the great principal types of animals involve him in a labyrinth of speculation and hypothesis in which he seeks in vain for conclusions of even an approximate certainty

Many other equally vigorous and well deserved criticisms of the embryological method might be cited but it should be emphasized that these criticisms are all directed against the application of the method to the solution of definite and concrete problems of descent and

relationship None of them denies and many strongly affirm that embryology affords some of the strongest and most convincing evidence in favor of the evolutionary theory

Let us examine some of this evidence To begin with it should be noted that in following out the ontogeny or individual development, the observer witnesses the formation of something new, not merely the enlargement and unfolding of a pre existing organism though the theory of *preformation* which was widely accepted in the eighteenth century, looked upon ontogeny precisely in that way as the growth of a germ which was the miniature of the parent. Such a theory was possible only before the development of microscopic technique had enabled the observer to detect the actual successive steps of change The egg is a single cell with the nucleus and all the parts of other undifferentiated cells though it may be enormously enlarged by the presence of food yolk In the hen s egg this food yolk is quite inert and the activity of development is confined to the minute disc of protoplasm on the outside of the yolk while in the frog s egg the yolk is disseminated though not uniformly throughout the egg and in the mammalian egg which is microscopic in size there is no yolk It is a very remarkable fact that all of the vertebrated animals fishes amphibians, reptiles birds and mammals however different their habits and modes of life have a mode of ontogeny which is of even more characteristically and unmistakably the same plan than is the type of their adult structure which was described in the last chapter The egg or the active portion of it divides in a definite and regular manner into a very large number of cells which arrange themselves in definite layers an outer and an inner and within these layers cell aggregates form incipient organs which step by step take on the adult condition Not only is the plan and type of development essentially similar throughout the whole phylum of the vertebrates but in accordance with the recapitulation theory many structural features which are permanent in lower forms appear in the embryos of higher and more advanced types In the latter however these features are transitory and in the course of development they either disappear or are so modified as to be very different sometimes unrecognizable in the adults

At a certain stage of the ontogeny the embryo of a mammal has gill pouches like a fish the skeletal supports of the gill pouches the arteries and veins which supply them with blood the structure of the heart in short the entire plan of the circulatory system is fish like

At a later stage most of the gill pouches have been obliterated, but one is retained and converted into the Eustachian canal which connects the throat with the middle ear inside of the ear drum Similarly the embryological evidence shows that the lungs of air breathers have been derived from the swim bladder of fishes a conclusion which had already been reached by comparative anatomy for in a remarkable

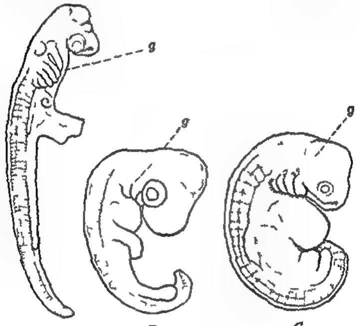


Fig. 29 —Embryos in corresponding stage of development of shark (A) fowl (B) and man (C) g gill slits (From Scott)

group known as the Dipnoi or lung fishes the air bladder is utilized for purposes of respiration

It has been objected that while embryology may prove relationship within a single type it fails to demonstrate any connection between different types, but this is not altogether true The Tunicata a curious group of marine animals once referred to the Mollusca, are shown by their ontogeny to be related to the vertebrates and the same is true of certain marine worms (*Balanoglossus*) Indeed most modern zoologists have adopted a scheme of classification in which

the type Chordata includes not only the true vertebrates but also the Lancelet (*Amphioxus*) the tunicates and *Balanoglossus* this scheme is founded upon the embryological evidence Among the inverte brates even more remarkable examples have been observed Such radically different types as the segmented worms and the shell fish (Mollusca) are brought into relationship by their ontogeny and their closely similar types of larvae, as are also though less distinctly the brachiopods or lamp shells and the Bryozoa The Horseshoe crab, or King-crab so abundant along our Atlantic coast was long of uncertain affinities, originally referred to the Crustacea largely because of its marine habits of life embryology makes much more probable its relationship to the air breathing scorpions and spiders a result which has been examined previously from another point of view in connection with blood tests

Even before the publication of Darwin's *Origin of Species* one of the great stumbling blocks in the way of the theory of special crea tion was the existence in a great many animals of rudimentary organs or such as are so far reduced and atrophied as to be of no service to their possessors An analogy employed by my lamented friend Mr Richard Lydekker may be advantageously repeated here Let us suppose that a screw steamer with longitudinal shaft leading aft from the engine room to the stern where it carries the propeller should on close examination reveal many signs that it has originally been a side wheeler or paddle boat Recognizable remnants of paddle boxes of bearings for a transverse shaft and the like are found what would be the inevitable conclusion? No one would maintain that a naval architect in possession of his senses in constructing a screw steamer would deliberately introduce features which are useful and appropriate only in a paddle boat The only reasonable explanation would be that the vessel had originally been built as a paddle-boat and had subsequently been converted into a screw steamer and in the conversion it had not been found necessary completely to eradicate all traces of the original construction Obviously the same reasoning applies to rudimentary organs The only satisfactory explanation of such useless remnants is that their possessors are descendants of ancestors in which those organs were fully functional It seems quite absurd to assume that in a separately and specially created animal useless structures reminiscent of other animals in which the same structures are useful and valuable should be included, merely to indicate ideal relationships and community of plan

It was sought to break the force of this very serious objection to the theory of special creation by saying that apparently useless organs may nevertheless have functions which are still unknown to us and may be revealed by future discovery In certain cases like that of the thyroid gland in the neck this contention has been justified but there are many others to which it does not apply For example in the great and varied whale tribe (order Cetacea) which includes the right, or whalebone, whales the sperm whales the porpoises dolphins, etc the forelimbs have been converted into swimming paddles but the hind limbs appear to have vanished completely leaving no externally visible trace Internally however recognizable remnants of the hind limb bones may be found in various stages of reduction which differ in the different members of the order In the Greenland Right Whale the hip-bone thigh bone and shin bone are indicated in the Finwhale only the hip bones and a minute rudiment of the thigh bone are to be found in the toothed whales only an almost unrecognizable remnant of the hip bone is left and in one of the dolphins even that has disappeared Similarly, the snakes have lost their limbs completely so far as external appearance is concerned and in most members of the group no trace of limbs is to be found on dissection but in certain snakes the rudiments of limbs are to be detected Leaving aside all preconceptions which is the more probable explanation of such phenomena, the theory of special creation or the theory of evolution?

Even if it were admitted that all rudimentary organs and structures found in the adult have a certain unknown use and value, no one could maintain this with regard to the countless instances of structures which are developed in the embryo but disappear entirely before birth It is possible to mention but a very few of such instances out of the great number that have already been observed and recorded but these few will suffice to illustrate the principle involved

' Examples of this may be cited from the most widely different groups in the embryo of insects especially of beetles pairs of legs are formed within the egg not only on the head and thorax, but also on the abdomen but while those on the head are transformed into mouth parts those on the thorax are farther developed in their jointing and musculature to be locomotive legs those on the abdomen are again resorbed In many fresh water worms the eggs of which are laid in a cocoon, from which they are hatched as a finished minute, crawling worm larval organs are nevertheless formed which recall those of the Trochophore the larva of the original worms which swims

freely in the sea However these larval organs are never properly functional since no actually free swimming larva is developed but the embryo merely floats in the albuminous fluid of the cocoon

' A particularly beautiful example is offered by the whales in their embryological development which has been thoroughly studied by Kukenthal In the adult condition they show only the anterior extremities, but in the embryo the posterior pair with their skeletal parts are formed, but are afterwards completely atrophied ' Although they are mammals, in the adult condition they have absolutely no covering of hair since in their aquatic life another and more effective protection against loss of heat is given by means of a thick layer of blubber, only a few coarse bristles partly with particular functions have persisted on a few parts of the body But in the embryo a dense covering of hair is formed which is later transformed in a peculiar manner and atrophied Further, a series of whales have no teeth in the adult condition but only the well known eel trap-like, horny plates from which whale bone is produced Nevertheless in the embryo there is a dentition of numerous teeth which are however resorbed without ever piercing the gum

Throughout the great group of the ruminants which includes the oxen buffaloes bison sheep goats antelopes deer and giraffes the collar bone is invariably lacking since it is superfluous on account of the exclusively locomotive manner in which the fore legs are employed In the embryo sheep the collar bone is established and even to some extent ossified but is subsequently resorbed and disappears entirely No doubt the collar bone will be found in many other embryo ruminants when the proper examination shall have been made but its demonstrated presence in the foetal sheep is sufficiently striking In the higher mammals the number of teeth was originally 44 or 11 on each side of both upper and lower jaws but in most of the modern or existing groups of these higher mammals this number has been very considerably reduced through the suppression of certain teeth We have every rea on to believe that the ancestors of the forms with reduced dentition possessed teeth in full numbers and that there has actually been a loss of teeth in the course of descent This conclusion is abundantly confirmed by the facts of embryology Take for example the great group of the gnawing mammals or Rodentia in which the front teeth or incisors above and below are reduced to one on each side except in the rabbits The incisors are chisel shaped and

Otto Maas *Die Abstammungslehre* pp 273–74

are faced with hard enamel so that the action of the upper teeth upon the lower keeps the cutting edges extremely sharp these teeth do not form roots but continue to grow throughout the lifetime of the animal Between the chisel like incisors and the grinding teeth there is a long toothless gap which we assume was in the ancestors of the rodents occupied by the second and third incisors the canine and two or more grinders This conclusion is justified by the facts of embryology for instance in the embryo of the squirrel several of the missing teeth are begun as distinct tooth germs but fail to develop never cut the gum and are resorbed before birth

All available evidence points to the conclusion that birds are descended from reptiles a conclusion which is especially strengthened by the facts of palaeontology and will be examined more at length in the following lecture Such a descent explains many otherwise puzzling features in the ontogeny of birds in which reptilian characteristics appear in transitory fashion and are either modified so as to take on typically bird like character or are suppressed altogether A remarkable example of this is the formation of rudimentary teeth in certain embryonic birds followed by their resorption and disappearance before hatching

It can hardly be contended that these rudimentary structures which are confined to the embryonic stages of development and of which no trace remains in the adult are so indispensable to the processes of ontogeny that they were specially created to serve this temporary purpose For such a contention there is not a particle of evidence and the theory of evolution which regards these structures as useless remnants due to inheritance from ancestors in which the structures are functional offers much the most satisfactory solution of the problem that has yet been suggested

Embryology further shows that evolution is not invariably an advance from lower and simpler to higher and more complex types but may be by way of degeneration and degradation The adoption of a parasitic mode of life is very apt to cause such degradation and some very remarkable instances of the degeneration of parasites have been observed An instructive example that may be cited is that of *Sacculina*, a nondescript creature that is parasitic on certain species of crabs The parasite is attached to the body of its victim underneath the tail by means of root like fibres which penetrate and ramify throughout the interior of the crab The root like fibres absorb nutriment and convey it to the body of the parasite which is reduced to a

mere bag without appendages; muscles, nervous system sensory apparatus digestive tract or any determinable organs save those of reproduction The creature has the power of assimilating the nutritive juices which are conveyed to it by the root like filaments from the body of its host and the power of reproduction and it must have some respiratory and excretory capacity though there are neither gills nor glands. From an examination of the adult parasite alone it would be quite impossible to classify it and determine the type and class to which it should be referred but embryology solves the problem From the egg is hatched a free swimming larva which has jointed appendages, nervous, muscular and digestive systems and in short clearly belongs to that group of the Crustacea which includes the barnacles This is degeneration carried nearly to the utmost possible extreme and yet the individual development shows the derivation of this otherwise problematical parasite and the steps through which it passed in its deterioration

It was stated above that several distinguished naturalists altogether reject the recapitulation theory as a means of interpreting the facts of embryology They do this on the ground that inasmuch as changes and innovations in form or structure must arise in the germ plasm at the very beginning of ontogeny there is no reason why such changes might not involve the whole course of embryological development To my mind this a priori objection to the recapitulation theory is quite without force in view of the great body of observed facts, but there is no time to enter upon a discussion of such an abstract and difficult problem For our present purpose however it is important to note that these objectors are staunch evolutionists and find in the community of mode in ontogeny between different classes of organisms one of the strongest arguments in support of the evolutionary doctrine.

CHAPTER X

EVIDENCES FROM PALAEONTOLOGY

STRENGTH AND WEAKNESS OF THE EVIDENCE

The word palaeontology means literally the science of ancient life. Practically, it is the study of the fossil remains of extinct animals and plants including any traces of their existence such as footprints, impressions in slate, clay, or coal The evidence from the fossils has definite elements of strength in that it deals with actual organisms that formerly inhabited the earth s surface Many of these species must have left descendants, some of which are doubtless living in a modified condition today Palaeontology should be able either strongly to support or to contradict the idea of evolution If its data accord with the evolution idea and are opposed to the special creation idea, the fossils may be said to be evidences of evolution

The weakness of the study of fossils lies in the fact that extremely few samples of the living forms that have existed in the past have been preserved and of those that have been preserved only a very small percentage have been dug up and studied by capable scientists Many types of animals and plants moreover, are soft and capable of preservation only under such exceptional conditions that but a rare specimen here and there over the world scattered through various widely separated strata has been found Only very common or abundant types are likely to have been preserved and discovered, for the chances of an uncommon form being preserved would be small and the further chances of these infrequently preserved specimens being found would be infinitely smaller

The great majority of fossil remains are fragmentary or preserved very incompletely, so that only the hard parts have come down to us There are, of course many important exceptions to this rule and these are our chief reliance in interpreting ancient life

That Darwin fully realized the vulnerable points in the palaeontological record is shown by the following quotation from the *Origin of Species*

' I look at the geological record as a history of the world imperfectly kept and written in a changing dialect, of this history we possess

the last volume alone, relating only to two or three countries Of this volume only here and there a short chapter has been preserved and of each page only here and there a few lines Each word of the slowly changing language, more or less different in the successive chapters, may represent the forms of life which are entombed in our successive formations and which falsely appear to us to have been abruptly introduced"

OTHER OPINIONS AS TO THE ADEQUACY OF THE EVIDENCES FROM PALAEONTOLOGY

"The primary and direct evidence in favour of evolution can be furnished only by palaeontology The geological record, so soon as it approaches completeness, must, when properly questioned yield either an affirmative or a negative answer if Evolution has taken place there will its mark be left, if it has not taken place there will lie its refutation"—T H Huxley

'*The geological record is not so hopelessly incomplete as Darwin* believed it to be Since *The Origin of Species* was written our knowledge of that record has been enormously extended and we now possess no complete volumes, it is true but some remarkably full and illuminating chapters The main significance of the whole lies in the fact that, *just in proportion to the completeness of the record is the unequivocal character of its testimony to the truth of the evolutionary theory*'—W B Scott

'On the other hand, matters have greatly improved since Darwin wrote his oft-cited Chapter X, many lands then geologically unknown have been explored and many of the missing chapters and paragraphs in the history of life have been brought to light The most ancient biologically intelligible period of the earth's history is called the Cambrian and, compared with the succeeding periods, the Cambrian has always been poor in fossils great areas and thicknesses of rocks being entirely barren No one could doubt that our knowledge of Cambrian life was most incomplete and inadequate A few years ago *Dr C D Walcott, Secretary of the Smithsonian Institution* discovered in the Canadian Rockies a most marvelous series of Cambrian fossils of an incredible delicacy and beauty of preservation which have thrown a flood of new and unexpected light into very dark places It is clear that the Cambrian seas swarmed with a great variety and profusion of life but that in only a few places so far known to us

were conditions such that these delicate creatures could be preserved It is not possible to say how far the difficulty caused by the imperfection of the geological record will be removed by the progress of discovery Even as matters stand to-day, the astonishing fact is that so much has been preserved rather than that the story is so incomplete Notwithstanding all the difficulties, the palaeontological method remains one of the most valuable means of testing the theory of evolution because certain chapters in the history of life have been recorded with a minuteness that is really very surprising — W B Scott *Theory of Evolution* (The Macmillan Company Reprinted by permission)

WHAT FOSSILS ARE AND HOW THEY HAVE BEEN PRESERVED

' Fossils are only animals and plants which have been dead rather longer than those which died yesterday —T H Huxley

' Fossils are either actual remains of bones or other parts preserved intact in soil or rocks or else and more commonly parts of animals which have been turned into stone or of which stony casts have been made All such remains buried by natural causes are called fossils ' — Jordan and Kellogg

FOSSILS CLASSIFIED

Class 1 The actual remains of recently extinct animals and plants which have been buried or surrounded by some sort of preserving material constitute the first type under consideration Such remains have undergone little or no change of the original organic matter into inorganic. Thus we find the complete bodies of great hairy mammoths frozen in the arctic ice These are so well preserved that dogs have fed upon their flesh Nearly a thousand species of extinct insects including many ants have been obtained practically intact from amber, a form of petrified resin Innumerable mollusk shells teeth of sharks pieces of buried logs bones of animals buried in asphalt lakes and bogs have been found in a well preserved condition

Class 2 Petrified fossils —The process of petrification involves the replacement particle for particle of the organic matter of a dead animal or plant by mineral matter So completely is the finer structure preserved that microscopic sections of preserved tissues especially of plants have practically the same appearance as sections made from living organisms Various mineral materials have been employed in petrification such as quartz limestone or iron pyrites

Class 3 **Casts and impressions**—Very frequently the animal or plant has been buried in mud or has lain on a soft mud flat only long enough to have left its impress in the plastic material Subsequently the entire organism has decayed and been dissolved away and its place has been taken by a mineral deposit Thus only the external appearance has been preserved as would be the case in making plaster-of paris casts Sometimes traceries of soft bodied animals have been left upon forming slate or coal that are almost as accurate in detail as a lithograph

Perhaps the most remarkable fossils known are those found by Professor Charles D Walcott in the marine oily shales of British Columbia A large number of soft bodied invertebrates of Cambrian age have been found so wonderfully preserved that not only are the external features revealed, but sometimes even the details of the internal organs may be seen through the transparent integument

Some authorities include among fossils such traces of extinct life as footprints utensils and tools of extinct man and even the vestiges of archaic sea beaches Perhaps this is stretching the definition of the term fossil too far

ON THE CONDITIONS NECESSARY FOR FOSSILIZATION

Examination and study of the rocks of the earth reveal the fact that fossils or the remains of animals and plants are found in certain kinds of rocks only They are not found in lava because lava comes from volcanoes and rifts in the earth's crust as a red hot viscous liquid which cools to form a hard rock No animal or plant caught in a lava stream will leave any trace Furthermore fossils are not found in granite nor in ores of metals nor in certain other of the common rocks Many rocks are like lava of igneous origin others, like granite although not originally in the melted condition have been so heated subsequent to their formation that any traces of animal or plant remains in them have been obliterated Fossils are found almost exclusively in rocks which have been formed by the slow deposition in water of sand clay, mud or lime The sediment which is carried into a lake or ocean by the streams opening into it sinks slowly to the bottom of the lake or ocean and forms there a layer which gradually hardens under pressure to become rock This is called sedimentary rock or stratified rock because it is composed of sedi

ment and sediment always arranges itself in layers or strata In sedimentary or stratified rocks fossils are found The commonest rocks of this sort are limestone sandstone and shales Limestone is formed chiefly of carbonate of lime sandstone is cemented sand, and shales, or slaty rocks, are formed chiefly of clay

' The formation of sedimentary rocks has been going on since land first rose from the level of the sea for water has always been wearing away rock and carrying it as sediment into rivers and rivers have always been carrying the worn-off lime and sand and clay downward to lakes and oceans at the bottoms of which the particles have been piled up in layers and have formed new rock strata But geologists have shown that in the course of the earth's history there have been great changes in the position and extent of land and sea Sea bottoms have been folded or upheaved to form dry land while regions once land have sunk and been covered by lakes and seas Again, through great foldings in the cooling crust of the earth which resulted in depression at one point and elevation at another, land has become ocean and ocean land And in the almost unimaginable period of time which has passed since the earth first shrank from its hypothetical condition of nebulous vapor to be a ball of land covered with water such changes have occurred over and over again They have however mostly taken place slowly and gradually The principal seat of great change is in the regions of mountain chains, which, in most cases are simply the remains of old folds or wrinkles in the crust of the earth

' When an aquatic animal dies it sinks to the bottom of the lake or ocean unless of course, its flesh is eaten by some other animal Even then its hard parts will probably find their way to the bottom There the remains will soon be covered by the always dropping sediment. They are on the way to become fossils Some land animals also might after death, get carried by a river to the lake or ocean and find their way to the bottom where they too, will become fossils or they may die on the banks of the lake or ocean and their bodies may get buried in the soft mud of the shores Or again they are often trodden in the mire about salt springs or submerged in quick sand It is obvious that aquatic animals are far more likely to be preserved as fossils than land animals. This inference is strikingly proved by fossil remains Of all the thousands and thousands of kinds of extinct insects mostly land animals, comparatively few specimens are known as fossils On the other hand the shell bearing

mollusks and crustaceans are represented in almost all rock deposits which contain any kind of fossil remains —Jordan and Kellogg

The study of geology teaches us that the earth s outer zones have undergone within the period of vertebrate history numerous profound changes which in general we may term climatic changes There have been periods of continental subsidence, accompanied by ocean floor elevations during which great continental plains have been covered with comparatively shallow seas The marine faunas of the seas have migrated into these shallows and representatives of them have been buried in sediment. When the reverse change has occurred and the continental plain has been again elevated the sedimentation of the shallow sea period forms a great rocky stratum laden with marine fossils Between periods of subsidence millions of years elapsed and therefore a break in the continuity of the entombed fossils is to be expected Discontinuity between the fossil faunas in adjacent strata is the invariable rule Were it not for this periodicity of subsidence and elevation there would be no boundaries between consecutive geologic strata

In addition to the methods of fossilization mentioned a few others deserve notice Many animals of the arid plains have been fossilized by becoming imbedded in dust or sand drifts which have piled up against rocky outcrops or have filled in dried up arroyos Some very valuable fossils have been recovered from asphaltic deposits as the result of animals falling into liquid or semiliquid lakes or pools of asphalt

Not only are external organs preserved with precision but even delicate internal structures such as the brains or the viscera of vertebrates have been found in such a perfectly natural shape that the comparative anatomy could be worked out with confidence

On the whole then we must conclude that the earlier pessimism regarding the inadequacy and insufficiency of fossil data is giving way before a steadily increasing optimism due to the very rapid advance in technique and the surprisingly abundant discoveries of the modern palaeontologist The more enthusiastic of the new school of fossil hunters do not despair of ultimately bringing to light all of the really essential links in the chain of evidence necessary to place the evolution theory beyond the reach of controversy

From D S Jordan and V L Kellogg *Evolution and Animal Life* (copyright 1907) Used by special permission of the publishers D Appleton & Company

ON THE LAPSE OF TIME DURING WHICH EVOLUTION IS BELIEVED TO HAVE TAKEN PLACE

Independently of our not finding fossil remains of such infinitely numerous connecting links (referring to the objection that all steps in the evolution of modern types should be revealed in the fossils) it may be objected that time cannot have sufficed for so great an amount of organic change all changes having been effected slowly It is hardly possible for me to recall to the reader who is not a practical geologist the facts leading the mind feebly to comprehend the lapse of time He who has read Sir Charles Lyell s grand work on the *Principles of Geology* which the future historian will recognize as having produced a revolution in natural science and yet does not admit how vast have been the past periods of time may at once close this volume . Not that it suffices to study the *Principles of Geology* or to read special treatises by different observers on separate formations and to mark how each author attempts to give an inadequate idea of the duration of each formation or even of each stratum We can l est g in some idea of past time by knowing the agencies at work and learning how deeply the surface of the land has been denuded and how much sediment has been deposited As Lyell has well remarked the extent and thickness of our sedimentary formations are the result and the measure of the denudation which the earth s crust has elsewhere undergone Therefore a man should examine for himself the great piles of superimposed strata and watch the rivulets bringing down the mud and the waves wearing away the sea-cliffs in order to comprehend something about the duration of past time, the monuments of which we see all around us —Charles Darwin *Origin of Species*

In 1862 says Schuchert[1] the physicist Lord Kelvin held that as our planet was continually losing energy in the form of heat the globe was a molten mass somewhere between 20 000 000 and 400 000 000 years ago with a probability of this state occurring about 98 000 000 years ago Finally in 1897 he concurred in Clarence King s conclusion that the globe was a molten mass about 24 000 000 years ago Both of these conclusions however were wrought out under the Laplacian hypothesis and now many geologists hold that the earth never was molten While geologists have not been able to fit their evidence into so short a time they have ever since been trying to keep their

[1] C. Schuch rt *Text-Bo k of Geology Part II Historical Geology* (1915)

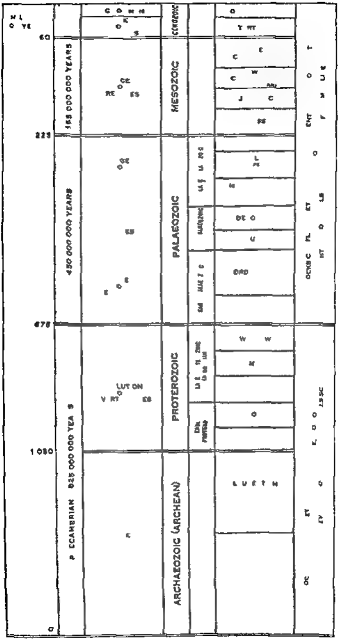


FIG. 50.—Total geologic time scale estimated at 1 500 000 000 years (*From Newman after Osborn*)

estimates within the bounds of Lord Kelvin's older calculations Walcott in 1893 on the basis of the stratigraphic record and the known discharge of sediment by rivers concluded that 70 000 000 years had elapsed since sedimentation began in the Archeozoic Sir Archibald Geikie places the time at 100 000 000 years and most geologists have tried although with difficulty to fit the record within these estimates

Since the discovery of radium all of the calculations previously made have been set aside by the new school of physicists and now the geologists are told they can have 1 000 000 000 or more years as the time since the earth attained its present diameter Even if finally it shall turn out that the physicists have to reduce their estimates as to the age of certain minerals and rocks geologists nevertheless appear to be on safer ground in accepting their estimates than those based either on sedimentation chemical denudation or loss of heat by the earth

The last decade has seen the demise of the outworn objection to evolution based on the idea that there has not been time enough for the great changes that are believed by evolutionists to have occurred Given 100 000 000 or 1 000 000 000 years since life began we can then allow 1 000 000 years for each important change to arise and establish itself We can also understand why it is that so little change can be noted in the majority of wild animals and plants within the historic period A thousand years in the development of the race is like a second in the development of an individual and though no one can notice any change in a growing creature in a second or a minute very radical changes can be noted in an hour or a day or a year We cannot see any movement in an hour hand of a clock but it moves with certainty around the dial in a relatively short time There is therefore no shortage of time Evolution may have been infinitely slow but time has been infinitely long The accompanying time scale shows the lapse of time and the distribution in time of the main groups of animals (Fig 3)

ON THE PRINCIPAL GENERAL FACTS REVEALED BY A STUDY OF THE FOSSILS

1 None of the animals or plants of the past are identical with those of the present The nearest relationship is between a few species of the past and some living species which have been placed in the same genera.

2 The animals and plants of each geologic stratum are at least generically different from those of any other stratum though belonging in some cases to the same families or orders

3 The animals and plants of the oldest (lowest) geologic strata represent all of the existing phyla, except the Chordata but the representatives of the various phyla are relatively generalized as compared with the existing types

4 The animals and plants of the newest (highest) geologic strata are most like those of the present and help to link the present with the past

5 There is in general a gradual *progression* toward higher types as one proceeds from the lower to the higher strata

6 Many groups of animals and plants reached the climax of specialization at relatively early geologic periods and became extinct

7 Only the less specialized relatives of the most highly specialized types survived to become the progenitors of the modern representatives of their group

8 It is very common to find a new group arising near the end of some geologic period during which vast climatic changes were taking place Such an incipient group almost regularly becomes the dominant group of the next period, because it developed under the changed conditions which ushered in the new period and was therefore especially favored by the new environment

9 The evolution of the vertebrate classes is more satisfactorily shown than that of any other group probably because they represent the latest phylum to evolve and most of their history coincides with the period within which fossils are known

10 Most of the invertebrate phyla had already undergone more than half of their evolution at the time when the earliest fossil remains were deposited

FOSSIL PEDIGREES OF SOME WELL KNOWN VERTEBRATES

PEDIGREE OF THE HORSE

Of all fossil pedigrees that of the horse is most often mentioned in evolutionary literature The main facts have been known for about forty years and there is a rather general consensus of opinion as to the history as a whole It appears practically certain that the horse family (Equidae) arose from a group of primitive five toed ungulates or hoofed mammals called Condylarthra that lived in Eocene times

No particular member of this extinct group has been found that fulfils all the requirements of a primitive horse ancestor so the chances are that the real ancestral condylarthran has not been discovered

The course of their [Equidae] evolution says Dendy,[1] has evidently been determined by the development of extensive dry grass-covered open plains on the American continent In adaptation to life on such areas structural modification has proceeded chiefly in two directions The limbs have become greatly elongated and the foot uplifted from the ground and thus adapted for rapid flight from pursuing enemies while the middle digit has become more and more important and the others together with the ulna and the fibula have gradually disappeared or become reduced to mere vestiges At the same time the grazing mechanism has been gradually perfected The neck and head have become elongated so that the animal is able to reach the ground without bending its legs and the cheek teeth have acquired complex grinding surfaces and have greatly increased in length to compensate for the increased rate of wear As in many other groups the evolution of these special characters has been accompanied by gradual increase in size Thus *Eohippus* of Lower Eocene times appears to have been not more than eleven inches high at the shoulder while existing horses measure about sixty four inches and the numerous intermediate genera for the most part show a regular progress in this respect

All these changes have taken place gradually and a beautiful series of intermediate forms indicating the different stages from *Eohippus* to the modern horse [*Equus*] have been discovered The sequence of these stages in geological time exactly fits in with the theory that each one has been derived from the one next below it by more perfect adaptation to the conditions of life Numerous genera have been described but it is not necessary to mention more than a few

The first indisputably horselike animal appears to have been *Hyracotherium* of the Lower Eocene of Europe Another Lower Eocene form is *Eohippus* which lived in North America probably having migrated across from Asia by the Alaskan land connection which was in existence at that time In *Eohippus* the fore foot had four completely developed hoofed digits and a thumb reduced to a splint bone in the hind foot the great toe had entirely disappeared and the little toe is represented by a vestigial structure or splint bone

[1] Arthur Dendy *Outlines of Evolutionary Biology* (D Appleton & Company 1916)

Then came in succession *Orohippus* of the Upper Eocene *Mesohippus* of the Lower Miocene *Pliohippus* of the Upper Pliocene and finally

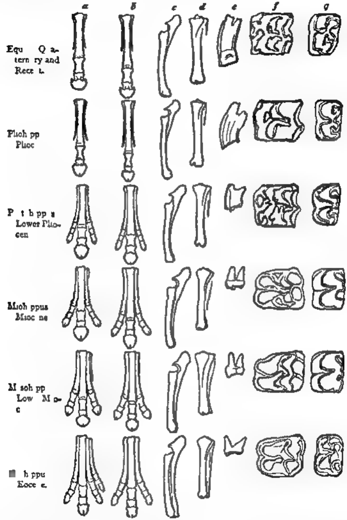


FIG 31 —Feet and teeth in fossil pedigree of the horse (*After Marsh*) *a* Bones of the fore foot *b* bones of the hind foot *c* radius and ulna *d* fibula and tibia *e* roots of a tooth *f* and *g* crowns of upper and lower teeth

Equus of the Quaternary and Recent Other genera might be mentioned but the history of this series has been pictured in a classic

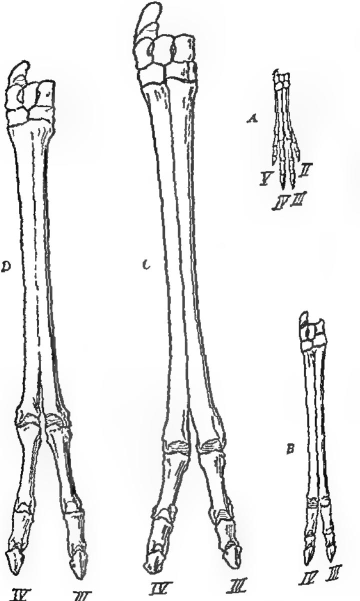


FIG 33 —Four stages in the evolution of the cameline fore foot *A Protylopus* Upper Eocene *B Poëbrotherium* Lower Oligocene *C Procamelus* Upper Miocene *D* guanaco Recent (*From Scott*)

Were there time enough to do so we might trace the development of this family backward, step by step through all the many stages between the Pleistocene and the Upper Eocene in quite as unbroken sequence and in as full detail as can be done for the horses. We must however pass over all the intermediate steps and consider the ancestral camels of the Upper Eocene These were very little animals hardly larger than a jack rabbit, which had the full complement of teeth 44 in total number, and all with very low crowns The limbs, and especially the feet, are relatively short, the ulna is complete and separate as is also the fibula there are four toes in each foot though the lateral pair of the hind foot are extremely slender, and there is no co-ossification to form cannon bones. The hoofs are well developed in form like those of an antelope so that there can have been no pad For the present, the line cannot be carried back of the Upper Eocene the probable ancestors from the middle and Lower Eocene being as yet, represented only by fragmentary specimens

In addition to this main stem of cameline descent which resulted in the modern species there were two short lived side branches which should be mentioned One ending in the Lower Miocene was the series descriptively called gazelle camels small animals with very long and slender legs evidently swift runners The other series the so-called giraffe camels terminated in the Upper Miocene these were browsers and display an increasing stature especially in the length of the neck and fore limbs They adapted themselves to the growing aridity of the western plains

EVOLUTION OF THE ELEPHANTS

A FRANKLIN SHULL

The mastodon elephant series shows a larger number of obvious changes than most of the other series named all of these changes except that of the body having to do with features of the head From the numerous specimens of elephant like forms available the following are selected (following Lull) as probably representing a direct line of evolution *Moeritherium* from the Upper Eocene of Egypt *Palaeomastodon* from the Lower Oligocene of Egypt also from India, *Trilophodon* from the Miocene of Europe Africa and North America *Mastodon* from the Pliocene and Pleistocene of

From A F Shull *Principles of Animal Biology* (copyright 1920) Used by special permission of the publishers The McGraw Hill Book Company

North America Europe and Asia *Stegodon* from the Pliocene of southern Asia and *Elephas* from the Pleistocene of the Americas Europe, and Asia as well as the living elephants of Asia and Africa

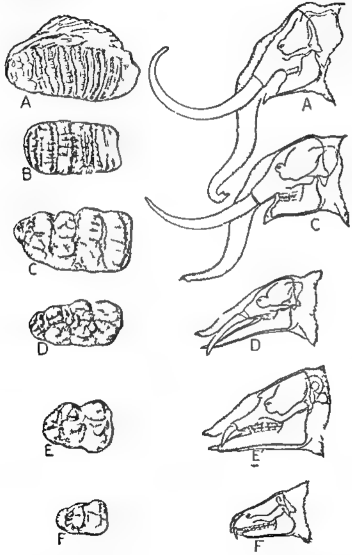


FIG 4 —Evolution of head and molar teeth of mastodons and elephants. *A* A *Elephas* Pleistocene *B* *Stegodon* Pliocene *C C* *Mastodon* Pleistocene *D D* *Trilophodon* Miocene *E E* *Palaeomastodon* Oligocene *F F* *Moeritherium* Eocene (*From Lull*)

A study of Figure 34 in connection with the following account will disclose the more striking steps of evolution These forms differed from one another in a number of features but the differences between any member of the series and the one that precedes or that which follows were so small that the series is obviously a continuous one *Moeritherium* was very different from the modern elephant but the intermediate forms completely bridged the gap The series exhibits an enormous increase in size of body changes in the form and size of the teeth a reduction in the number of teeth an alteration in the method of tooth succession the enlargement of certain teeth to become tusks the elongation and subsequent shortening of the lower jaw the development of the upper lip and nose into a proboscis and an increase in the height of the skull through the development of large cavities in the substance of the bone These features are described in the several forms seriatim

Moeritherium.—The earliest animal recognized as belonging to the elephant series *Moeritherium* by name was recovered from the late Eocene and early Oligocene deposits of northern Egypt It was slightly over three feet in height The features suggesting elephantine affinities are the high posterior portion of the skull (Fig 34, *F*), composed of somewhat cancellate bone that is bone containing open spaces the elongation of the second pair of incisors in each jaw to form short tusks the indication of transverse ridges on the molar teeth (Fig 34 *F*) and the position of the nasal openings some distance back of the tip of the upper jaw indicating probably a prehensile upper lip There were 24 teeth and the neck was long enough to enable the animal to put its head to the ground It probably fed upon tender shoots and swamp vegetation

Palaeomastodon—This form also lived in Egypt but has recently been found in India It dates from early Oligocene time *Palaeomastodon* was of somewhat larger size than the preceding form, the posterior part of the skull was distinctly higher (Fig 34 *E'*)—with a greater development of cancellate bone and the neck was somewhat shortened The upper incisors of the second pair were more elongated as tusks and bore a band of enamel on their front surfaces The lower second incisors were present but not enlarged All other incisors and the canines had disappeared The molar teeth (*E*) resembled those of *Moeritherium* but were larger The lower jaw was considerably elongated, and the total number of teeth was still high (26) The nasal openings had receded until they were just in front of the eyes

which is believed to indicate the existence of a short proboscis extending at least to the tips of the tusks

Trilophodon —*Trilophodon* a great migrant and consequently wide spread over several continents as stated above exhibited in several respects a striking advance over *Palaeomastodon* but this advance was in the main in the same direction as was indicated by the change from *Moeritherium* to *Palaeomastodon* *Trilophodon* was a huge animal nearly as large as modern Indian elephants The tusks were considerably longer (Fig 34, *D'*) and still bore a band of enamel The molar teeth were large and greatly reduced in number, so that only two were present at any one time on each side of each jaw The surface of these teeth bore a somewhat larger number of transverse crests (Fig 34 *D*) than were present in the earlier forms The lower jaw was enormously elongated so that it projected as far forward as the tusks The great weight of the lower jaw and tusks was associated with a considerable development of cancellate bone in the skull to which the supporting muscles of the neck were attached Presumably there was a proboscis which extended to or beyond the tips of the tusks and lower jaw

Mastodon —The mastodons on the whole represent a line of development which became extinct but in their incipient stages they appear to have given rise to the succeeding forms leading to the elephants The body was somewhat larger than that of *Trilophodon* being about the size of the Indian elephant The tusks (*C'*) were much elongated (9 feet or more) but the lower jaw was greatly shortened and the lower incisor teeth were reduced or wanting The molar teeth (Fig 34 *C*) were scarcely more complex than earlier forms, and numbered two on each side of each jaw They were still crushing teeth and the food must have been tender twigs and succulent plants indeed remains of such objects have been found in the region of the stomach of the fossil mastodons

Stegodon —This animal is of interest chiefly because the molar teeth bore five or six well defined transverse ridges (Fig 34 *B*) These ridges were due to plates of *enamel* extending up through the tooth and inclosing a substance known as *dentine* Over the enamel in an unworn tooth was a thin coat of a third substance called *cement*, but there was not much of this substance between the ridges In the latter respect *Stegodon* differed as is pointed out below from the elephants and mammoths On the whole *Stegodon* was intermediate between the mastodons and elephants

Elephas—In this genus are included a number of extinct forms (the mammoths) from three or four continents and the living elephants The extinct forms though called mammoths were not large animals being no larger than the Indian elephant of today, and not so large as the living African species Some of the features of the elephants, their size, the short neck the long proboscis and the heavy tusks are matters of common observation The skull is very high and short (Fig 34 A) The height is due chiefly to the development of cancellate bone, not to the enlargement of the brain which is still quite small. As stated above the high skull affords the necessary leverage for the muscles that support the weight of the tusks The molar teeth are distinctly grinding teeth (Fig 34 A) Each tooth bears a number of transverse ridges about ten in the African elephant and two dozen or more in the Indian species These ridges are worn down by the chewing of harsh food so that the upper surface displays a number of flattened tubular plates of enamel inclosing dentine and bound together by cement A tooth is completely worn out by use and is replaced by another The method of replacement however is peculiar While the tusks (incisors) are of two sets one following the other like milk and permanent teeth of other mammals the grinders succeed one another in continuous fashion There are never more than two visible grinders on each side of each jaw As they wear out they move forward in the jaw and are replaced by new teeth appearing behind New molars thus enter at intervals of two to four years in young elephants and at intervals of 15 to 30 years in later life If an elephant lives long enough (60 years or more) it develops a total of 28 teeth including tusks but has not more than ten (often less) at any one time

Correlated with the nature of the teeth of the elephants are their food and chewing habits Whereas the ancestral forms whose molars bore prominent elevations lived on twigs and tender herbage which they crushed in mastication the mammoths with their flattened tooth surfaces devoured grasses sedges and other harsh vegetation which they ground with lateral motion of the teeth upon one another In this respect modern elephants are like the mammoths

In the changes described above is found one of the most beautiful and best established evolutionary series with which the palaeontologist is acquainted Only a few others equal or approach it in clearness and completeness

CHAPTER XI

THE EVOLUTION OF MAN PALAEONTOLOGY[1]

RICHARD SWANN LULL

ORIGIN OF PRIMATES

Stock —There is but little doubt that two important orders of modern mammals the Carnivora and the Primates had a common origin diverging mainly along lines determined by a dietary contrast as the former have become more strictly flesh eating or predaceous the latter largely fruit eating and as a consequence more completely arboreal Back of each group lie as annectant forms the Insectivora not perhaps such as are alive to day, as all these are highly specialized along diverse lines but generalized insectivores possessing because of their primitiveness a wider range of potential adaptation Matthew is disposed to think of these, our distant ancestors at the dawn of the Tertiary as a sort of hybrid between a lemur and a mongoose rather catholic in their tastes living among and partly in the trees with sharp nose bright eyes and a shrewd little brain behind them looking out if you will from a perch among the branches upon a world that was to be singularly kind to them and their descendants Thus we can define the stock as a relatively large brained arboreal insectivore of primitive but adaptable dentition and especially of progressive mentality

Time —The time of primate origin must have been not later than basal Eocene, as primates clearly definable as such are found in the Lower Eocene rocks of both Europe and North America

Place —The simultaneous appearance of the primate in the Old World and the New gives rise to the same conclusions as to their place of origin and their migrations thence as with other modernized mammals It suffices now to say that their ancestral home was boreal Holarctica probably within the limits of the present continent of Asia whence they migrated southward along the three great continental radii The impelling cause of this migration was the increasing northern cold before which the boreal limitations of the tropical forests retreated carrying with them the primates which, in

[1] From R. S Lull *Organic Evolution* (copyright 1917) Used by special permission of the publishers The Macmillan Company

general are utterly dependent upon such an environment for their sustenance

Geologic record.—Primates are found in the North American sediments from Lower to Upper Eocene time, when they became extinct Thus, while their remains constitute a relatively large percentage of the total fauna of the Eocene, primates are utterly unknown on this continent from that time until the coming of man In Europe the record is similar except that the extinction occurred at a somewhat later date the Oligocene Furthermore they reappear in Europe in the Lower Miocene at the time of the proboscidean migration out of Africa whence these primates may also have come Their second European extinction was in the Upper Pliocene shortly before the first appearance of mankind

But in southern Asia Africa and South America the evolution of primates seems to have been continuous since the first great southward migration The evidence however is not so much the historical *documents as the presence of primates in those places at the present* time the fossil record is not entirely lacking although highly incomplete The South American monkeys may have had their origin in the ancient North American primates, or more doubtfully the stock may have come by way of Africa Scott inclines toward the latter view although he says the evidence is by no means conclusive

ORIGIN OF MAN

Stock—According to W K Gregory the stock from which man arose was some big brained anthropoid related most nearly to the chimpanzee gorilla group an assumption based upon anatomical evidences in spite of wide differences in habitus and consequent adaptation

Place—Evidences point to central Asia as the place of descent from the trees of the human precursor the reasons for this belief being several First, it was central for migrations elsewhere Europe on the other hand where the most conclusive in fact almost the exclusive evidence for fossil man is found is too small an area for the divergent evolution of the several human species Second Asia is contiguous to the oldest known human remains which as we shall see were found in Java Third it was the seat of the oldest civilizations not only of the existing nations which like the Chinese trace their recorded history back to a hoary antiquity but of nations which preceded them by thousands of years and whose records have not yet come to light

This antiquity vastly exceeds that of the nations of Europe or of the Americans or of Africa Fourth central Asia is the source of almost all of our domestic animals, many of which have been subjected to human will and control for thousands of years and this is equally true of many of our domestic plants This is not due to the fact that man first reached civilization in Asia but rather that he chose for his companions the highest and best of their several evolutionary lines and Asia was the place of all others upon earth where the evolution in general of organic life reached its highest development in late Cenozoic time (Williston) Fifth climatic conditions in Asia in the Miocene or early Pliocene were such as to compel the descent of the prehuman ancestor from the trees a step which was absolutely essential to further human development

Impelling cause —We look for a geologic cause back of this most momentous crisis in the evolution of humanity and we find it in continental elevation and consequent increasing aridity of climate, especially to the northward of the Himalayas With this increased aridity and tempering of tropical heat came the dwindling of the forested areas suitable to primate occupancy Barrell has suggested that this diminution left residual forests comparable to the diminishing lakes and ponds of the Devonian which upon final desiccation compelled their denizens to become terrestrial or perish The dwindling of the residual forests would have an effect upon the tree-dwellers which may be expressed in precisely the same words. Once upon the ground the effect upon even a conservative type—and the primates in general where constant conditions prevail are slow of change—would be the rapid acquisition of such adaptations as were necessary to insure survival under the new conditions The other man like apes had, unfortunately for their further evolution, reached a region where tropical forests continued to be available and hence have retained their arboreal life and with it a stagnation of progress The result has been at any rate on the part of the three larger forms a degeneracy from the estate of their common ancestry with mankind the gibbons seem to have deteriorated less while terrestrial man has risen to the summit of primate evolution

Time —The time of the descent is not later than early Pliocene nor earlier than Miocene time, when the terrestrial ape man became what we would call human was perhaps later, but certainly during the Pliocene which makes the age of man as such measurable in terms of hundreds of thousands of years!

Significance of the descent from trees —As a result of the descent from the trees certain definite factors were called into play, each of which had its effect on the further evolution Briefly enumerated these are (1) Assumption of the erect posture, (2) liberation of the hands from their ancient locomotor function to become organs of the mind (3) loss of the easily obtainable food of the tropical forests necessitating the search for sustenance, both plant and animal and man became a hunter, (4) need of clothing with increasing inclemency of the weather, especially during the long winters (5) freedom from climatic restrictions—when an omnivorous diet and clothing were acquired man was no longer limited to one definite habitat and the result was dispersal (6) the development of communal life rendered possible by the terrestrial habitat Primates are at best gregarious submitting as in the gorilla to the leadership of the strongest male but it is only by communal life with its attendant division of labor that man can rise above the level of utter savagery

Evolutionary changes —Human evolutionary changes which are recorded are more erect posture shorter arms perfection of thumb opposability reduction of muzzle and of size of teeth loss of jaw power development of chin prominence increase in skull capacity, diminution of brow ridges diminution in strength of zygo matic or temporal arch increase in size and complexity of brain especially frontal lobes, development of articulate speech

FOSSIL MAN

Fossil remains of man are found under two conditions in river valley deposits and in limestone caverns which served first as a dwelling place and later as a sepulture Of these the caverns have been by far the most productive but they contain only the remains of the later races as the caverns according to Penck did not become available for human occupancy before middle Pleistocene time.

The rarity of human fossils may be explained first by the various burial customs which seldom are sufficiently perfect to preclude the possibility of alternate wetting and drying or of rapid oxidation both of which are prohibitive of fossilization If man lived and died in the forests the chances for his fossilization in common with other forest creatures was very remote for the remains of such are almost invari ably destroyed by other animals by dampness or by fungi and rarely attain a natural burial in sediment If on the other hand he dwelt

in the open, the chances of so shrewd a creature being caught in the flood waters and thus buried in sediment were not very great However we account for it the fact remains that relics of ancient man are rare and are valued accordingly

In North America —Repeated instances of seemingly ancient man have been brought to light in North America such as the Calaveras skull' of the California gold bearing gravels which was satirized by Bret Harte the Nebraska Loess man,' and those of the Trenton gravels none of which with the possible exception of the last mentioned has proved to be really old in the geologic sense Indirect evidence of human antiquity, that is the association of North American man with animals which are now extinct while very rare has been reported in at least two highly authentic instances The first of these was at Attica New York and is attested by Doctor John M Clarke, the New York state geologist Four feet below the surface of the ground in a black muck he found the bones of the mastodon (*Mastodon americanus*) and 12 inches below this in undisturbed clay pieces of pottery and thirty fragments of charcoal The charcoal may have been of natural origin but the presence of the pottery seems conclusive The other instance was that of the remains of a herd of extinct bison (*Bison antiquus*) found near Smoky Hill River Logan County, Kansas, and thus described by Professor Williston An arrow head was found underneath the right scapula of the largest skeleton, embedded in the matrix but touching the bone itself The skeleton was lying upon the right side The bone bed when cleared off contained the skeletons of five or six adult animals and two or three younger ones together with a foetal skeleton within the pelvis of one of the adult skeletons The animals had evidently all perished together during the winter There was no possibility of the accidental intrusion of the arrow head in the place where found It must have been within the body of the animal at the time of death, or have been lying on the surface beneath its body

What at this writing is claimed to be another genuine case of such an association this time of the actual human bones has just been announced from Florida This find which has been reported by State Geologist Sellards was made at Vero eastern Florida in 1913 The fossil human bones are from two incomplete skeletons and are found in strata which also contain remains of the following extinct species *Elephas columbi Equus leidyi* a fox, a deer the ground sloth *Megalonyx jeffersoni* and the American mastodon

In South America —A number of finds have been recorded from South America notably by the late Florentino Ameghino of Buenos Aires who contributed so largely to our knowledge of South American prehistoric life An expert from Washington, Doctor Ales Hrdlicka, has studied with the utmost care the locality and character of each of these finds in the Western World and has expressed the opinion that none is of an antiquity greater than that of the pre-Columbian Indians

Further evidence lies in the uniformity of type, except for minor distinctions of all native American peoples There is no such racial differentiation as that seen in the Old World and the argument is that there has not been time for such a deployment The area and conditions as an adaptive radiation center are surely ample

In Africa —The only African relics thus far reported are those of prehistoric cultures comparable to those of Southern Europe in certain caverns of the Barbary States There has also been reported from Oldoway ravine German East Africa a human skeleton of undoubted antiquity It is described however as being neither a very early nor a primitive type

In Asia —Asia has given us in *Pithecanthropus* the oldest known relic of the Hominidae found at Trinil in the island of Java Osborn says It is possible that within the next decade one or more of the Tertiary ancestors of man may be discovered in northern India among the foothills known as the Siwaliks . Such discoveries have been heralded but none have thus far been actually made Yet Asia will probably prove to be the center of the human race We have now discovered in southern Asia primitive representatives or relatives of the four existing types of anthropoid apes namely the gibbon, the orang the chimpanzee and the gorilla and since the extinct Indian apes are related to those of Africa and of Europe it appears probable that southern Asia is near the center of the evolution of the higher primates and that we may look there for the ancestors not only of prehuman stag s like the Trinil race but of the higher and truly human types

In Europe —It is in Europe however that the tale of human prehistory is the most complete not only through the happy accident of preserval but because it has been much more thoroughly explored than has the Asiatic evolutionary center The latter however, holds the greatest hopes for future exploration since, as we have emphasized Europe is too small to be an adaptive radiation center and European

prehistoric man represents waves of migration from the greater continent

Nevertheless the European record has enabled us to name and define a number of distinct human species and here the record of the cultural evolution of man is also unusually complete Hence European chronology is taken as a standard in describing discoveries from any portion of the world

CHRONOLOGICAL TABLE

(Adapted from Osborn 1915)

POSTGLACIAL TIME	5 000 years
Upper Palaeolithic culture	
Crô-Magnon man	
FOURTH GLACIAL STAGE (Wurm Wisconsin)	50 000 years
Close of Lower Palaeolithic culture	
Neanderthal man	
THIRD INTERGLACIAL STAGE	150 000 years
Beginning of Lower Palaeolithic culture	
Piltdown and pre Neanderthaloid men	
THIRD GLACIAL STAGE (Riss Illinoian)	175 000 years
SECOND INTERGLACIAL STAGE	375 000 years
Heidelberg man	
SECOND GLACIAL STAGE (Mindel Kansas)	400 000 year
FIRST INTERGLACIAL STAGE	475 000 years
Pithecanthropus ape man	
FIRST GLACIAL STAGE (Gunz Nebraskan)	500 000 years

Pithecanthropus —The Java ape man *Pithecanthropus erectus* (Fig 35) was discovered in Trinil on the Solo or Bengawan River in central Java in 1894 The type consists of a calvarium or skull cap a left thigh bone, and two upper molar teeth The skull is characterized by its limited capacity about two-thirds that of man and by the low flat forehead and beetling brows Hence not only was the brain limited in its total size but this was especially true of the frontal lobes which as we have seen are the seat of the higher intellectual faculties Thus as Osborn says, although touch, taste and

FIG 35 —Skull of Java ape man *Pithecanthropus erectus* (From Lull after Dubois)

vision were well developed there was a limited faculty for profiting by experience and accumulated tradition The femur associated with the skull is remarkable for its length and slight curvature as compared with the primitive Neanderthal race of Europe and indicates a creature fully as erect and nearly as tall as the average European of today the height being estimated at 5 feet 7 inches as compared with 5 feet 3 inches for the Neanderthals and 5 feet [illegible] inches the average height of modern males The erect posture of course implies the liberation of the hands from any part in the locomotor function The teeth are somewhat ape like but are more human than are those of the gibbon and the human mode of mastication has been acquired Certain authorities have tried to prove that *Pithecanthropus* is nothing but a large gibbon, but the weight of authority considers it prehuman though not in the line of direct development into humanity It is nevertheless a highly important transitional form

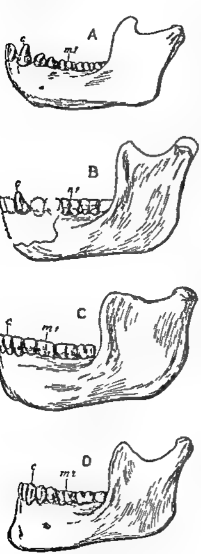


FIG 36 —Jaws left outer aspect of *A* chimpanzee *Pan* sp *B* fossil chimpanzee *Pan vetus* found in association with Piltdown man *C* Heidelberg man *Homo heidelbergensis* *D* modern man *H sapiens* (From Lull, after Woodward)

Associated with the *Pithecanthropus* remains are those of a number of the contemporary animals which fix the date as either of the Upper Pliocene or lowermost Pleistocene period which being rendered in terms of years gives an estimated age of about 500 000

Heidelberg man—*Homo heidelbergensis* the Heidelberg man represents the oldest recorded European race, geologically speaking The type was discovered in 1907 in river sands, 79 feet below the surface, at Mauer near Heidelberg, South Germany The relic consists of a perfect lower jaw with the dentition (Fig 36, *C*) The description by the discoverer, Doctor Schoetensack follows (from Osborn)

The mandible shows a combination of features never before found in any fossil or recent man The protrusion of the lower jaw just below the front teeth (the chin prominence) which gives shape to the human chin is entirely lacking Had the teeth been absent it would have been impossible to diagnose it as human From a fragment of the symphysis of the jaw it might well have been classed as some gorilla like anthropoid while the ascending ramus resembles that of some large variety of gibbon The absolute certainty that these remains are human is based on the form of the teeth—molars premolars canines and incisors are all essentially human and although somewhat primitive in form show no trace of being intermediate between man and the anthropoid apes but rather of being derived from some older common ancestor The teeth however are small for the jaw the size of the border would allow for the development of much larger teeth We can only conclude that no great strain was put on the teeth and therefore the powerful development of the bones of the jaw was not designed for their benefit The conclusion is that the jaw regarded as unquestionably human from the nature of the teeth ranks not far from the point of separation between man and the anthropoid apes In comparison with the jaws of the Neanderthal races we may consider the Heidelberg jaw as pre-Neanderthaloid it is in fact a generalized type

Associated with the Heidelberg jaw is an extensive warm-climate fauna straight tusked elephant (*E antiquus*) Etruscan rhinoceros primitive horse bison wild cattle (*urus*) bear lion and so on, all of which aid in establishing the date of the jaw as Second Interglacial and its age conservatively estimated at from 300,000 to 375 000 years The cultural evolution of Heidelberg man is indicated by the presence of eoliths flint implements of the crudest workmanship if indeed their apparent fashioning is not merely the result of use

Neanderthal man.—The original specimen of the Neanderthal man, *Homo neanderthalensis* or *primigenius* (Figs 37, 38 39) was discovered in 1856 not far from Düsseldorf in Rhenish Prussia Here the valley of the Düssel forms the deep Neanderthal ravine whose

limestone walls are penetrated by caverns in one of which the remains were found What was doubtless a perfect skeleton at the time of its

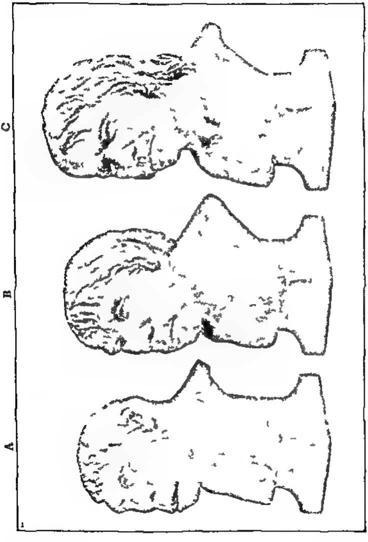


FIG 37 —Restoration of prehistoric men after models by J H McGregor A *Pithecanthropus erectus* the ape man of Java B *Homo neanderthalensis* the Neanderthal man of Europe C *Homo sapiens* the Cro-Magnon man of Europe (*From Lull by courtesy of Professor McGregor*)

discovery was so injured by its finders that only a portion of it which is now preserved in the Provincial Museum at Bonn was saved This prophet of an unknown race was for a time utterly without honor

though of course the subject of a most heated controversy being considered as non human or as Virchow believed, owing its distinctive characters to disease. The sagacity of Huxley threw true light upon the problem, though it was not until the mute testimony of other representatives of the race (the men of Spy) was offered that even Huxley's masterful conception of the Neanderthal characters was taken as an accepted fact

Professor Huxley's description of the Neanderthal type is classic. He says

"The anatomical characters of the skeletons bear out conclusions which are not flattering to the appearance of the owners. They were short of stature but powerfully built with strong curiously curved thigh bones the lower ends of which are so fashioned that they must have walked with a bend at the knees

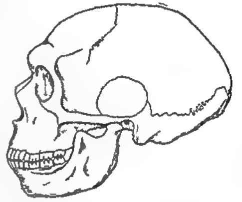


FIG 38—Neanderthaloid skull of La Chapelle aux Saints (*Homo neanderthalensis*) (*From Lull after Boule*)

Their long depressed skulls had very strong brow ridges; their lower jaws of brutal depth and solidity sloped away from the teeth downwards and backwards in consequence of the absence of that especially characteristic feature of the higher type of man the chin prominence

Subsequently several more specimens have come to light at Spy in Belgium at Krapina in Croatia at Le Moustier La Chapelle aux Saints and La Ferrassie in France, and at Gibraltar, which, while differing in various details effectually serve to establish the race whose main characteristics are Heavy overhanging brows retreating forehead, long upper lip jaw less powerful than that of the Heidelberg man but very thick and massive chin generally strongly receding but in process of forming; dentition extraordinarily massive in the La Chapelle specimen whereas in those of Spy the teeth are small. The skull in many characteristics is nearer to the anthropoids than to modern man

The brain is large and its volume is surely human, but the proportions are again less like those of recent man than like the anthropoids. The chest is large and robust, the shoulders broad, and

the hand large but the fingers are relatively short the thumb lacking the range of movement seen in modern man The knee was some what bent the leg powerful with a short shin and clumsy foot clearly not of cursorial adaptation The curve of the bent leg was correlated with a *similar curvature of the* spine so that the man could not stand fully erect as he lacked the fourth or cervical curvature of *Homo sapiens* The average stature was 5 feet 3 inches with a range from 4 feet 10 3 inches to 5 feet 5 2 inches partly sex differences

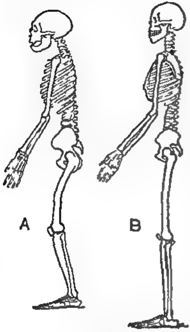


FIG 39 —Skeleton of Neanderthal man *A Homo neanderthalensis* compared with that of a living native Australian *B Homo sapiens* the latter the lowest existing race (*From Lull after Woodward*)

Neanderthal man lived in Europe from the Third Interglacial stage through the Fourth Glacial a duration of thousands of years and then became extinct, from twenty to twenty five millenniums ago He seems to have been an actual lineal successor of the man of Heidelberg but was throughout his long career an unprogressive static race One of the most remarkable features in connection with this race, however was the very reverent way in which the dead were buried with an abundance of ornaments and finely worked flints This can have but one interpretation the awakening within this ancient type of the instinctive belief in immortality!

Piltdown man—*In 191* was announced the discovery of a very ancient man from the Thames gravels at Piltdown Sussex England Here again the skull was injured and partly lost so that the question of its proper restoration has been the subject of considerable controversy The material consists of portions of the cranial walls nasal bones a canine tooth and part of a lower jaw The brain case in this instance is typically human except for the remarkably thick cranial walls The forehead is high and lacks the superorbital ridges of Neanderthal man and *Pithecanthropus* While the skull is of com

paratively high human type the associated jaw and canine tooth clearly a e not and some difficulty was met in explaining their evolu tionary discrepancy That has apparently been answered, however, by the conclusion that the association of the material is purely acci dental and that the jaw not only does not belong with the skull, but that it is not even human but is that of a fossil chimpanzee That being the case there seems to be no reason for the exclusion of the Piltdown man who has been named *Eoanthropus dawsoni* from the direct line of human ancestry The specimen is not, perhaps, so surely dated as are those of the other European races, but it is associated with a warm-climate fauna and is generally considered to belong to the Third Interglacial stage—from 100 000 to 150 000 years old and hence vastly more ancient than the more primitive *Homo neander thalensis* (See Fig 36, *B*)

Crô Magnon man —The original finds of the men of the Crô Magnon race *Homo sapiens* were made at Gower Wales, and at Aurignac France In the latter place seventeen skeletons came to light in 1852 but were buried in the village cemetery and thus lost to science and not until 1868, when five more skeletons were discovered at Crô-Magnon France was the race established These individuals an old man two young men, a woman and a child are thus the types of the race This magnificent race is thus characterized

Skull large but narrow, with a broad face hence disharmonic. Facial angle equalling the highest type of *Homo sapiens* Jaw thick and strong with a narrow but very prominent chin Forehead high and orbital ridges reduced Brain not only of high type but very large, that of the women exceeding the average male of to-day

The stature of the old man was 6 feet 4 5 inches, the average for males being 6 feet 1 5 inches, for women 5 feet 5 inches a great dis parity The lower segments of the limbs were long in contrast with the Neanderthal type hence the men of Crô-Magnon were swift footed while those of Neanderthal were slow Osborn says ' The wide, short face, the extremely prominent cheekbones the spread of the palate and a tendency of the upper cutting teeth and incisors to project forward and the narrow, pointed chin recall a facial type which is best seen to-day in tribes living in Asia to the north and to the south of the Himalayas As regards their stature the Crô-Magnon race recall the Sikhs living to the south of the Himalayas In the disharmonic proportions of the face that is the combination of broad cheekbones and narrow skull, they resemble the Eskimo The

sum of the Crô-Magnon characters is certainly Asiatic rather than African, whereas in the Grimaldis (of which specimens have been found in association with Crô-Magnons at the Grotte des Enfants Mentone) the sum of the characters is decidedly negroid or African '

The Crô-Magnons again show by their elaborate burial customs how old and well founded is the belief in life after death They are supposed to be the people who left on the walls of the caverns of France and Spain the marvelous examples of Upper Palaeolithic art of which Professor Osborn's book gives so adequate a description They lived for a while contemporaneously with the men of Neanderthal and may have contributed somewhat to the final extinction of the latter In the course of time, however, they too declined, although to this day survivors of the race may be seen in Dordogne at Landes near the Garonne in Southern France and at Lannion in Brittany Osborn says

The decline of the Crô Magnons with their artistic culture, may have been partly due to environmental causes and the abandonment of their vigorous nomadic mode of life or it may be that they had reached the end of a long cycle of psychic development We know as a parallel that in the history of many civilized races a period of great artistic and industrial development may be followed by a period of stagnation and decline without any apparent environmental cause

Europe was repopulated after Crô-Magnon decline by later invaders from the Asiatic realm the so-called Mediterranean narrow headed and the Alpine broad headed types, etc, probably differentiated in Asia in early Palaeolithic times The repopulation took place in the Upper Palaeolithic

EVIDENCES OF HUMAN ANTIQUITY

Great variation.—These, briefly summarized are first great variation If man is monophyletic that ■ derived from a single prehuman species and there is no reason to believe otherwise he must be old for while the adaptations to ground-dwelling after the descent from the trees were doubtless relatively rapidly acquired the differentiation into the various races due perhaps largely to climatic influences rather than to any notable environmental change must have been slowly attained As corroborative evidence we have but to point to the mural paintings on Egyptian monuments dating back

several thousand years in which are depicted the Ethiopian Caucasian and the like which are in some instances striking likenesses of the present day Egyptians

Universal distribution is, in animals another mark of antiquity in man, it is probably less so because of his greater intelligence And yet before transportation had become a science man s spread over land and sea was extremely slow

High intelligence as compared with that of the anthropoids is also a mark of antiquity for the brain especially the type of brain found in the higher human races must have been very slow of development Our study of fossil man shows this

Communal life, division of labor and all of the complicated interactions which it brings about and the development of law and religions all have taken time When we realize that Babylonian texts twice as remote as the patriarch Abraham, give evidence of highly perfect laws and of a civilization which must have antedated their production by centuries we gain another yet more emphatic impression of human antiquity Add to all this the palaeontological evidence of man s association with various genera and numerous successive species of prehistoric animals of which he alone survives and the evidence is complete

FUTURE OF HUMANITY

Because of his intelligence and communal co operation man is no longer subject to the laws which govern the adaptation of animals to their environment Osborn s law of adaptive radiation which as we have seen, applies equally well to the insects reptiles and mammals fails in its application to mankind and yet man has become as thoroughly adapted to speed, flight to the fossorial and aquatic as they but his adaptation is artificial and to a very small extent only affects his physical frame while theirs is natural and the stamp of environment is deeply impressed upon the organism

Man s physical evolution has virtually ceased but in so far as any change is being effected, it is largely retrogressive Such changes are Reduction of hair and teeth, and of hand skill and dulling of the senses of sight smell and hearing upon which active creatures depend so largely for safety That sort of charity which fosters the physically, mentally, and morally feeble and is thus contrary to the law of natural selection must also in the long run have an adverse effect upon the race

Man is hardly as yet subject to Malthus law for while he is increasing more rapidly than any other animal owing largely to the care of the young which makes the expectation of life of the new born relatively very high his migratory ability, but above all his intelligence save him from the application of the law A single new discovery such as that of electricity may increase his food supply and other life necessities several fold His future evolution in so far as it is progressive will be mental and spiritual rather than physical, and as such will be the logical conclusion of the marvelous results of organic evolution.

Sinanthropus pekinensis

A remarkable new discovery has come to light during the last few years and deserves to be added to the foregoing account by Professor Lull the discovery of Pekin man *Sinanthropus pekinensis* Next to *Pithecanthropus* in the fossil series of primitive man and only a stage more advanced is this newly discovered genus A few years ago Professor Davidson Black found some fossil teeth near Pekin China which though distinctively human were different enough from any others known to be assigned to a new genus of man Search for further remains in the same neighborhood brought to light two lower jaws containing the kind of teeth discovered by Black The investigation was climaxed a little later when the Chinese anthropologist W C Pei unearthed in the same neighborhood a complete cranium At last reports collectors had brought in parts of skeletons of at least ten individuals While *Sinanthropus* is more like *Pithecanthropus* than any other extinct genus of man it is a more advanced type and helps materially to bridge the gap between *Pithecanthropus* and the higher human genera At this writing further details about this new genus would be inappropriate since investigations upon it are still in progress

CHAPTER XII

EVIDENCES FROM GEOGRAPHIC DISTRIBUTION

PRINCIPLES OF GEOGRAPHIC DISTRIBUTION

Just as palaeontology may be said to be a study of the vertical distribution (distribution in time) of organisms so geographic distribution may be called a study of the horizontal distribution of organisms on the earth s surface at any given time (spatial distribution) We are chiefly to be concerned with the *present* spatial distribution of animal and plant species but equally interesting studies have been and still may be made of the horizontal or contemporaneous existence of extinct forms Much new knowledge has been gained by combining the data of palaeontology with those of geographic distribution. In fact neither field can be studied profitably without recourse to the other This fact was clearly perceived by J A Thomson in his little manual on *Evolution* when he combined the two types of evidence in one chapter under the title Evidences of Evolution from Explorer and Palaeontologist

It was a consideration of the present and of the past distribution of Edentates that led Charles Darwin to his first clear concept of descent with modification In his voyage on the Beagle he found that present day Edentates (armadillos sloths anteaters), a very peculiar group of archaic mammals are practically confined to South America When he also found that the only fossil Edentates resembling but also differing from the existing types are also confined to South America he easily arrived at the only inference permitted by the facts that the present Edentates are the modified descendants of the Edentates of the past.

The following quotations from both an older and a recent writer will give the reader a clear idea of the ways in which the general facts of geographic distribution bear witness to the truth of the evolutionary principle

The theory says Wallace[1] which we may now take as established—that all the existing forms of life have been derived from other forms by a natural process of descent with modification and that this same process has been in action during past geological time—should

[1] From A. R Wallace *Darwinism* (1889) Used by special permission of the publishers The Macmillan Company

enable us to give a rational account not only of the peculiarities of form and structure presented by animals and plants but also of their grouping together in certain areas and their general distribution over the earth s surface

"In the absence of any exact knowledge of the facts of distribution a student of the theory of evolution might naturally anticipate that all groups of allied organisms would be found in the same region and that as he travelled farther and farther from any given centre, the forms of life would differ more and more from those which prevailed at the starting point till in the remotest regions to which he could penetrate he would find an entirely new assemblage of animals and plants altogether unlike those with which he was familiar He would also anticipate that diversities of climate would always be associated with a corresponding diversity in the forms of life

' Now these anticipations are to a considerable extent justified Remoteness on the earth s surface is usually an indication of diversity in the fauna and flora while strongly contrasted climates are always accompanied by a considerable contrast in the forms of life But this correspondence is by no means exact or proportionate and the converse propositions are often quite untrue Countries which are near to each other often differ radically in their animal and vegetable productions while similarity of climate together with moderate geographical proximity, are often accompanied by marked diversities in the prevailing forms of life Again while many groups of animals—genera families and sometimes even orders—are confined to limited regions most of the families many genera and even some species are found in every part of the earth An enumeration of a few of these anomalies will better illustrate the nature of the problem we have to solve

"As examples of extreme diversity, notwithstanding geographical proximity, we may adduce Madagascar and Africa whose animal and vegetable productions are far less alike than are those of Great Britain and Japan at the remotest extremities of the great northern continent while an equal or perhaps even a still greater diversity exists between Australia and New Zealand. On the other hand Northern Africa and South Europe though separated by the Mediterranean Sea have faunas and floras which do not differ from each other more than do the various countries of Europe As a proof that similarity of climate and general adaptability have had but a small part in determining the forms of life in each country we have the fact of the enormous increase

of rabbits and pigs in Australia and New Zealand, of horses and cattle in South America and of the common sparrow in North America though in none of these cases are the animals natives of the countries in which they thrive so well. And lastly in illustration of the fact that allied forms are not always found in adjacent regions we have the tapirs which are found only on opposite sides of the globe in tropical America and the Malayan Islands the camels of the Asiatic deserts whose nearest allies are the llamas and alpacas of the Andes and the marsupials only found in Australia and on the opposite side of the globe in America Yet again, although mammalia may be said to be universally distributed over the globe, being found abundantly on all the continents and on a great many of the larger islands yet they are entirely wanting in New Zealand, and in a considerable number of other islands which are nevertheless perfectly able to support them when introduced

Now most of these difficulties can be solved by means of well known geographical and geological facts. When the productions of remote countries resemble each other there is almost always continuity of land with similarity of climate between them When adjacent countries differ greatly in their productions we find them separated by a sea or strait whose great depth is an indication of its antiquity or permanence. When a group of animals inhabits two countries or regions separated by wide oceans it is found that in past geological times the same group was much more widely distributed and may have reached the countries it inhabits from an intermediate region in which it is now extinct We know also, that countries now united by land were divided by arms of the sea at a not very remote epoch while there is good reason to believe that others now entirely isolated by a broad expanse of sea were formerly united and formed a single land area There is also another important factor to be taken account of in considering how animals and plants have acquired their present peculiarities of distribution—changes of climate We know that quite recently a glacial epoch extended over much of what are now the temperate regions of the northern hemisphere and that consequently the organisms which inhabit those parts must be comparatively speaking recent immigrants from more southern lands But it is a yet more important fact that down to middle Tertiary times at all events an equable temperate climate with a luxuriant vegetation extended to far within the Arctic circle over what are now barren wastes covered for ten months of the year with snow and ice The

Arctic zone has therefore, been in past times capable of supporting almost all of the forms of life of our temperate regions and we must take account of this condition of things whenever we have to speculate on the possible migration of organisms between the old and new continents.

Many of the facts of distribution, says Shull "are capable of interpretation by the assumption that evolution has operated with the other factors. If each kind of animal has arisen from a pre-existing kind then each group of related animals must have had an ancestral form and if the component parts of the groups are widespread the range of the ancestral form may be considered to be the center of dispersal of the group The facts of distribution can apparently be interpreted only on this basis

"Accepting evolution along with the other factors which can be recognized the method of distribution is generally conceived to be as follows The ancestral form tends to spread in all directions In some directions it is limited by unfavourable conditions either throughout its life or for some time. In other directions it extends its range Anywhere within its range new types of individuals may arise through the process of evolution These new types may be fitted to occupy new regions and if they are formed near the limits of the range they may find opportunity to spread into areas which are inaccessible to the unaltered members of the species Thus may arise recognizably distinct forms coincident in range with certain environmental conditions If particular forms or the individuals of a single form are accidentally (or possibly by sporadic migration) transferred across barriers the distribution of the group becomes discontinuous If these processes have been going on for a long time that is if the common ancestors of a group of forms existed long ago the range may have had time to become very extensive or its discontinuity very marked If contrariwise the ancestors were comparatively recent the range is likely to be much smaller For this reason groups that have diverged far enough to have attained the rank of families are on the whole more widespread than those so nearly allied as to be considered genera Should the environment become altered within a given range, the occupying form might be driven from it or destroyed

From A F Shull *Principles of Animal Biology* (copyright 1920) Used by special permission of the publishers, The McGraw Hill Book Company

If the environment in a region adjoining a range should change in a favourable manner the range might be extended at that point without any alteration on the part of the animals

The distribution of animals is inferred to be in harmony with this method which involves it will be noted the factors of migration evolution physiological and morphological dependence upon the environment the diversity and changeableness of the earth s surface and extinction and in this manner are explained the differences in geographical position differences in size of range, differences in the continuity of range and the fact that ranges are at first continuous, differences in physical and biological conditions which characterize the ranges of different forms and the geographical proximity of apparently related forms

SOME OF THE MORE SIGNIFICANT FACTS ABOUT THE DISTRIBUTION OF ANIMALS

THE FAUNA OF OCEANIC ISLANDS

GEORGE JOHN ROMANES

Turning now from aquatic organisms to terrestrial the body of facts from which to draw is so large that I think the space at my disposal may be best utilized by confining attention to a single division of them—that namely which is furnished by the zoological study of oceanic islands

In the comparatively limited—but in itself extensive—class of facts thus presented we have a particularly fair and cogent test as between the alternative theories of evolution and creation For where we meet with a volcanic island hundreds of miles from any other land and rising abruptly from an ocean of enormous depth we may be quite sure that such an island can never have formed part of a now submerged continent In other words we may be quite sure that it always has been what it now is—an oceanic peak separated from all other land by hundreds of miles of sea and therefore an area supplied by nature for the purpose as it were of testing the rival theories of creation and evolution For let us ask upon these tiny insular specks of land what kind of life should we expect to find? To this question the theories of special creation and of gradual evolution would agree in giving the same answer up to a certain point For both theories would agree in supposing that these islands would at all

From G J Romanes *Darwin and after Darwin* (copyright 1893) Used by special permission of The Open Court Publishing Company

events in large part derive their inhabitants from accidental or occasional arrivals of wind blown or water floated organisms from other countries—especially of course from the countries least remote But after agreeing upon this point, the two theories must part company in their anticipations The special creation theory can have no reason to suppose that a small volcanic island in the midst of a great ocean should be chosen as the theatre of any extraordinary creative activity or for any particularly rich manufacture of peculiar species to be found nowhere else in the world On the other hand the evolution theory would expect to find that such habitats are stocked with more or less peculiar species For it would expect that when any organisms chanced to reach a wholly isolated refuge of this kind their descendants should forthwith have started upon an independent course of evolutionary history Protected from intercrossing with any members of their parent species elsewhere, and exposed to considerable changes in their conditions of life it would indeed be fatal to the general theory of evolution if these descendants during the course of many generations, were not to undergo appreciable change It has happened on two or three occasions that European rats have been accidentally imported by ships upon some of these islands and even already it is observed that their descendants have undergone a slight change of appearance so as to constitute them what naturalists call local varieties The change of cour e is but slight because the time allowed for it has been so short But the longer the time that a colony of a species is thus completely isolated under changed conditions of life the greater, according to the evolution theory should we expect the change to become Therefore in all cases where we happen to know from independent evidence of a geological kind that an oceanic island is of very ancient formation the evolution theory would expect to encounter a great wealth of peculiar species On the other hand as I have just observed the special creation theory can have no rea on to suppose that there should be any correlation between the age of an oceanic island and the number of p culiar species which it may be found to contain

Therefore having considered the principles of geographical distribution from the widest or most general point of view we shall pass to the opposite extreme and con ider exhaustively or in the utmost possible detail the facts of such distribution where the conditions are best suited to this purpose—that is as I have already said upon oceanic islands which may be metaphorically regarded as having been

formed by nature for the particular purpose of supplying naturalists with a crucial test between the theories of creation and evolution The material upon which my analysis is to be based will be derived from the most recent works upon geographical distribution—especially from the magnificent contributions to this department of science which we owe to the labours of Mr Wallace Indeed all that follows may be regarded as a condensed filtrate of the facts which he has collected Even as thus restricted however, our subject matter would be too extensive to be dealt with on the present occasion were we to attempt an exhaustive analysis of the floras and faunas of all oceanic islands upon the face of the globe Therefore, what I propose to do is to select for such exhaustive analysis a few of what may be termed the most oceanic of oceanic islands—that is to say those oceanic islands which are most widely separated from main lands and which therefore, furnish the most unquestionable of test cases as between the theories of special creation and genetic descent

Azores —A group of volcanic islands nine in number about 900 miles from the coast of Portugal and surrounded by ocean depths of 1 800 to 2 500 fathoms There is geological evidence that the origin of the group dates back at least as far as Miocene times There is a total absence of all terrestrial Vertebrata other than those which are known to have been introduced by man Flying animals, on the other hand are abundant namely 53 species of birds one species of bat, a few species of butterflies moths and hymenoptera, with 74 species of indigenous beetles All these animals are unmodified European species with the exception of one bird and many of the beetles Of the 74 indigenous species of the latter 36 are not found in Europe but 19 are natives of Madeira or the Canaries, and 3 are American doubtless transplanted by drift wood The remaining 14 species occur nowhere else in the world though for the most part they are allied to other European species There are 69 known species of land shells of which 37 are European and 32 peculiar though all allied to European forms Lastly there are 480 known species of plants of which 40 are peculiar though allied to European species

Bermudas.—A small volcanic group of islands 700 miles from North Carolina. Athough there are about 100 islands in the group their total area does not exceed 50 square miles The group is surrounded by water varying in depth from 2 500 to 3,800 fathoms The

only terrestrial Vertebrate (unless the rats and mice are indigenous) is a lizard allied to an American form, but specifically distinct from it and therefore a solitary species which does not occur anywhere else in the world. None of the birds or bats are peculiar, any more than in the case of the Azores but as in that case a large percentage of the land shells are so—namely at least one quarter of the whole. Neither the botany nor the entomology of this group has been worked out but I have said enough to show how remarkably parallel are the cases of these two volcanic groups of islands situated in different hemispheres but at about the same distance from large continents. In both there is an extraordinary paucity of terrestrial Vertebrata and of any peculiar species of bird or beast. On the other hand there is in both a marvellous wealth of peculiar species of insects and land shells. Now these correlations are all abundantly intelligible. It is a difficult matter for any terrestrial animal to cross 900 or even 700 miles of ocean therefore only one lizard has succeeded in doing so in one of the two parallel cases, and living cut off from intercrossing with its parent form the descendants of that lizard have become modified so as to constitute a peculiar species. But it is more easy for large flying animals to cross those distances of ocean: consequently, there is only one instance of a peculiar species of bird or bat—namely a bull finch in the Azores which being a small land bird is not likely ever to have had any other visitors from its original parent species coming over from Europe to keep up the original breed. Lastly, it is very much more easy for insects and land mollusca to be conveyed to such islands by wind and floating timber than it is for terrestrial mammals or even than it is for small birds and bats but yet such means of transit are not sufficiently sure to admit of much recruiting from the mainland for the purpose of keeping up the specific types. Consequently the insects and the land shells present a much greater proportion of peculiar species—namely one half and one fourth of the land shells in the one case and one eighth of the beetles in the other. All these correlations I say are abundantly intelligible on the theory of evolution but who shall explain on the opposite theory why orders of beetles and land mollusca should have been chosen from among all other animals for such superabundant creation on oceanic islands so that in the Azores alone we find no less than 32 of the one and 14 of the other? And in this connection I may again allude to the peculiar species of beetles in the island of Madeira. Here there are an enormous number of peculiar species though they are nearly all related to

or included under the same genera as beetles on the neighboring continent Now as we have previously seen no less than 200 of these species have lost the use of their wings Evolutionists explain this remarkable fact by their general laws of degeneration under disuse and the operation of natural selection as will be shown later on but it is not so easy for special creationists to explain why this enormous number of peculiar species of beetles should have been deposited on Madeira all allied to beetles on the nearest continent, and nearly all deprived of the use of their wings And similarly of course with all the peculiar species of the Bermudas and the Azores For who will explain on the theory of independent creation why all the peculiar species both of animals and plants which occur on the Bermudas should so unmistakably present American affinities while those which occur on the Azores no less unmistakably present European affinities? But to proceed to other and still more remarkable cases

The Galapagos Islands—This archipelago is of volcanic origin situated under the equator between 500 and 600 miles from the West Coast of South America The depth of the ocean around them varies from 2 000 to 3 000 fathoms or more This group is of peculiar interest from the fact that it was the study of its fauna which first suggested to Darwin s mind the theory of evolution I will therefore begin by quoting a short passage from his writings upon the zoological relations of this particular fauna

Here almost every product of the land and of the water bears the unmistakable stamp of the American continent There are twenty six land birds of these twenty one or perhaps twenty three are ranked as distinct species and would commonly be assumed to have been here created yet the close affinity of most of these birds to American species is manifest in every character in their habits gestures and tones of voice So it is with the other animals and with a large proportion of the plants as shown by Dr Hooker in his admirable Flora of this archipelago The naturalist looking at the inhabitants of these volcanic islands in the Pacific, distant several hundred miles from the continent feels that he is standing on American land Why should this be so? Why should the species which are supposed to have been created in the Galapagos Archipelago and nowhere else bear so plainly the stamp of affinity to those created in America? There is nothing in the conditions of life in the geological nature of the islands in their height or climate or in the proportions in which the several classes are associated together which closely resembles the

conditions [illegible] distribution [illegible] de Verne [illegible] in their [illegible] Facts such as [illegible] any view of [illegible] turned [illegible] Africa [illegible]

The following [illegible] species [illegible] a peculiar [illegible] South American [illegible] that [illegible] hence [illegible] species, of which [illegible] of them [illegible] However, [illegible] beautiful [illegible] what forms they are [illegible] and [illegible] distinctive [illegible] United States [illegible] in the [illegible] during the [illegible] currently and [illegible] in the Caribbean [illegible] date the [illegible] of [illegible] sufficiently often [illegible] than of the [illegible] more they differ from any other [illegible] American continent, the more [illegible] nearer relations among those South American [illegible]

more restricted range and therefore the least likely to have found their way to the islands with any frequency

The insect fauna of the Galapagos Islands is scanty and chiefly composed of beetles These number 35 species which are nearly all peculiar and in some cases go to constitute peculiar genera The same remarks apply to the twenty species of land shells Lastly of the total number of flowering plants (332 species) more than one half (174 species) are peculiar It is observable in the case of these peculiar species of plants—as also of the peculiar species of birds—that many of them are restricted to single islands It is also observable that with regard both to the fauna and flora the Galapagos Islands as a whole are very much richer in peculiar species than either the Azores or Bermudas notwithstanding that both the latter are considerably more remote from the nearest continents This difference which at first sight appears to make against the evolutionary interpretation really tends to confirm it For the Galapagos Islands are situated in a calm region of the globe unvisited by those periodic storms and hurricanes which sweep over the North Atlantic and which every year convey some straggling birds insects seeds etc to the Azores and Bermudas Notwithstanding their somewhat greater isolation geographically therefore the Azores and Bermudas are really less isolated biologically than are the Galapagos Islands and hence the less degree of peculiarity on the part of their endemic species But on the theory of special creation it is impossible to understand why there should be any such correlation between the prevalence of gales and a comparative inertness of creative activity And as we have seen it is equally impossible on this theory to understand why there should be a further correlation between the *degree* of peculiarity on the part of the isolated species and the *degree* in which their nearest allies on the mainland are there confined to narrow ranges and therefore less likely to keep up any biological communication with the islands

St. Helena —A small volcanic island ten miles long by eight wide situated in mid-ocean 1 100 miles from Africa and 1,800 from South America It is very mountainous and rugged bounded for the most part by precipices rising from ocean depths of 17 000 feet, to a height above the sea level of nearly 3 000 When first discovered it was richly clothed with forests but these were all destroyed by human agency during the 16th 17th and 18th centuries The records of civilization present no more lamentable instance of this kind of destruction

From a merely pecuniary point of view the abolition of these primeval forests has proved an irreparable loss but from a scientific point of view the loss is incalculable These forests served to harbour countless forms of life which extended at least from the Miocene age and which having found there an ocean refuge survived as the last remnants of a remote geological epoch In those days as Mr Wallace observes St Helena must have formed a kind of natural museum or vivarium of archaic species of all classes the interest of which we can now only surmise from the few remnants of those remnants which are still left among the more inaccessible portions of the mountain peaks and crater edges These remnants of remnants are as follows

There is a total absence of all indigenous mammals reptiles fresh water fish and true land birds There is however a species of plover allied to one in South Africa but it is specifically distinct and therefore peculiar to the island The insect life on the other hand is abundant. Of beetles no less than 129 species are believed to be aboriginal, and, with one single exception the whole number are peculiar to the island 'But in addition to this large amount of specific peculiarity (perhaps unequalled anywhere else in the world) the beetles of this island are remarkable for their generic isolation and for the altogether exceptional proportion in which the great divisions of the order are represented The species belong to 39 genera of which no less than 25 are peculiar to the island and many of these are such isolated forms that it is impossible to find their allies in any particular country [Wallace] More than two thirds of all the species belong to one group of weevils—a circumstance which serves to explain the great wealth of beetle population the weevils being beetles which live in wood and St Helena having been originally a densely wooded island This circumstance is also in accordance with the view that the peculiar insect fauna has been in large part evolved from ancestor which reached the island by means of floating timber for of course no explanation can be suggested why special creation of this highly peculiar insect fauna should have run so disproportionately into the production of weevils About two-thirds of the whole number of beetles or over 80 species show no close affinity with any existing insects while the remaining third have some relations though often very remote with European and African forms That this high degree of peculiarity is due to high antiquity is further indicated, according to our theory by the large number of species which some of the types comprise Thus the 54 species of *Cossonidae* may be

referred to three types the 11 species of *Bembidium* form a group by themselves and the *Heteromera* form two groups "Now each of these types may well be descended from a single species which originally reached the island from some other land, and the great variety of generic and specific forms into which some of them have diverged is an indication and to some extent a measure, of the remoteness of their origin [Wallace] But on the counter supposition that all these 128 peculiar species were separately created to occupy this particular island, it is surely unaccountable that they should thus present such an arborescence of natural affinities amongst themselves

Passing over the rest of the insect fauna which has not yet been sufficiently worked out we next find that there are only 20 species of indigenous land shells—which is not surprising when we remember by what enormous reaches of ocean the land is surrounded Of these 20 species no less than 13 have become extinct three are allied to European species while the rest are so highly peculiar as to have no near allies in any other part of the globe So that the land shells tell exactly the same story as the insects

Lastly the plants likewise tell the same story The truly indigenous flowering plants are about 50 in number besides 26 ferns Forty of the former and ten of the latter are peculiar to the island and as Sir Joseph Hooker tells us cannot be regarded as very close specific allies of any other plants at all Seventeen of them belong to peculiar genera and the others all differ so markedly as species from their congeners that not one comes under the category of being an insular form of a continental species So that with respect to its plants no less than with respect to its animals we find that the island of St Helena constitutes a little world of unique species allied among themselves but diverging so much from all other known forms that in many cases they constitute unique genera

Sandwich Islands—*These are an extensive group of islands* larger than any we have hitherto considered—the largest of the group being about the size of Devonshire The entire archipelago is volcanic with mountains rising to a height of nearly 14 000 feet The group is situated in the middle of the North Pacific at a distance of considerably over 2 000 miles from any other land and surrounded by enormous ocean depths The only terrestrial vertebrata are two lizards, one of which constitutes a peculiar genus There are 24 aquatic birds five of which are peculiar four birds of prey two of which are peculiar and 16 land birds all of which are peculiar

Moreover these 16 land birds constitute no less than 10 peculiar genera and even one peculiar family of five genera This is an amount of peculiarity far exceeding that of any other islands and of course corresponds with the great isolation of this archipelago The only other animals which have here been carefully studied are the land shells and these tell the same story as the birds For there are no less than 400 species which are all without any exception peculiar while about three-quarters of them go to constitute peculiar genera Again of the plants 620 species are believed to be endemic and of these 377 are peculiar, yielding no less than 39 peculiar genera

THE FAUNA OF CONTINENTAL ISLANDS—MADAGASCAR AND NEW ZEALAND[1]

A. R. WALLACE

The two exceptions just referred to are Madagascar and New Zealand and all the evidence goes to show that in these cases the land connection with the nearest continental area was very remote in time The extraordinary isolation of the productions of Madagascar—almost all the most characteristic forms of mammalia birds and reptiles of Africa being absent from it—renders it certain that it must have been separated from that continent very early in the Tertiary if not as far back as the latter part of the Secondary period and this extreme antiquity is indicated by a depth of considerably more than a thousand fathoms in the Mozambique Channel though this deep portion is less than a hundred miles wide between the Comoro Islands and the main land Madagascar is the only island on the globe with a fairly rich mammalian fauna which is separated from a continent by a depth greater than a thousand fathoms and no other island presents so many peculiarities in these animals or has preserved so many lowly organised and archaic forms The exceptional character of its productions agrees exactly with its exceptional isolation by means of a very deep arm of the sea

New Zealand possesses no known mammals and only a single species of batrachian but its geological structure is perfectly continental There is also much evidence that it does possess one mammal although no specimens have been yet obtained Its reptiles and birds are highly peculiar and more numerous than in any truly oceanic island Now the sea which directly separates New Zealand from Australia is more than 2 000 fathoms deep but in a north west direc

[1] From A R Wallace *Darwinism* (copyright 1889) Used by special permission of the publishers The Macmillan Company

tion there is an extensive bank under 1 000 fathoms, extending to and including Lord Howe s Island while north of this are other banks of the same depth approaching towards a submarine extension of Queensland on the one hand and New Caledonia on the other, and altogether suggestive of a land union with Australia at some very remote period Now the peculiar relations of the New Zealand fauna and flora with those of Australia and of the tropical Pacific Islands to the northward indicate such a connection probably during the Cretaceous period and here again, we have the exceptional depth of the dividing sea and the form of the ocean bottom according well with the altogether exceptional isolation of New Zealand an isolation which has been held by some naturalists to be great enough to justify its claim to be one of the primary Zoological Regions

THE DISTRIBUTION OF MARSUPIALS

A R WALLACE

This singular and lowly organised type of mammals constitutes almost the sole representative of the class in Australia and New Guinea while it is entirely unknown in Asia, Africa or Europe It reappears in America where several species of opossums are found and it was long thought necessary to postulate a direct southern connection of these distant countries in order to account for this curious fact of distribution. When however we look to what is known of the geological history of the marsupials the difficulty vanishes In the Upper Eocene deposits of Western Europe the remains of several animals closely allied to the American opossums have been found and as at this period a very mild climate prevailed far up into the arctic regions there is no difficulty in supposing that the ancestors of the group entered America from Europe or Northern Asia during early Tertiary times

But we must go much further back for the origin of the Australian marsupials All the chief types of the higher mammalia were in existence in the Eocene if not in the preceding Cretaceous period and as we find none of these in Australia that country must have been finally separated from the Asiatic continent during the Secondary or Mesozoic period Now during that period in the Upper and the Lower Oolite and in the still older Trias the jaw bones of numerous small mammalia have been found forming eight distinct genera which

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are believed to have been either marsupials or some allied lowly forms In North America also in beds of the Jurassic and Triassic formations the remains of an equally great variety of these small mammalia have been discovered and from the examination of more than sixty specimens, belonging to at least six distinct genera Professor Marsh is of the opinion that they represent a generalised type from which the more specialised marsupials and insectivora were developed

From the fact that very similar mammals occur both in Europe and America at corresponding periods and in beds which represent a long succession of geological time and that during the whole of this time no fragments of any higher forms have been discovered it seems probable that both the northern continents (or the larger portion of their area) were then inhabited by no other mammalia than these with perhaps other equally low types It was probably not later than the Jurassic age when some of these primitive marsupials were able to enter Australia where they have since remained almost completely isolated and being free from the competition of higher forms they have developed into the great variety of types we now behold there These occupy the place and have to some extent acquired the form and structure of distinct orders of the higher mammals—the rodents the insectivora and the carnivora—while still preserving the essential characteristics and lowly organisation of the marsupials At a much later period—probably in late Tertiary times—the ancestors of the various species of rats and mice which now abound in Australia and which with the aerial bats constitute its only forms of placental mammals entered the country from some of the adjacent islands For this purpose a land connection was not necessary as these small creatures might easily be conveyed among the branches or in the crevices of trees uprooted by floods and carried down to the sea and then floated to a shore many miles distant That no actual land connection with or very close approximation to an Asiatic island had occurred in recent times is sufficiently proved by the fact that no squirrel pig civet or other widespread mammal of the Eastern hemisphere has been able to reach the Australian continent

THE DI TRIBUTION OF BIRDS

A. R WALLACE

These vary much in their powers of flight and their capability of traversing wide seas and oceans Many swimming and wading birds

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can continue long on the wing fly swiftly and have, besides the power of resting safely on the surface of the water These would hardly be limited by any width of ocean except for the need of food and many of them as the gulls petrels and divers find abundance of food on the surface of the sea itself These groups have a wide distribution *across* the oceans while waders—especially plovers sandpipers snipes, and herons—are equally cosmopolitan, travelling *along* the coasts of all the continents and across the narrow seas which separate them Many of these birds seem unaffected by climate and as the organisms on which they feed are especially abundant on arctic temperate and tropical shores there is hardly any limit to the range even of some of the species

Land birds are much more restricted in their range owing to their usually limited powers of flight, their inability to rest on the surface of the sea or to obtain food from it and their greater specialisation which renders them less able to maintain themselves in the new countries they may occasionally reach Many of them are adapted to live only in woods or in marshes or in deserts, they need particular kinds of food or a limited range of temperature and they are adapted to cope only with the special enemies or the particular group of competitors among which they have been developed Such birds as these may pass again and again to a new country but are never able to establish themselves in it and it is this organic barrier as it is termed rather than any physical barrier, which, in many cases, determines the presence of a species in one area and its absence from another We must always remember therefore, that although the presence of a species in a remote oceanic island clearly proves that its ancestors must at one time have found their way there the absence of a species does not prove the contrary since it also may have reached the island but have been unable to maintain itself owing to the inorganic or organic conditions not being suitable to it This general principle applies to all classes of organisms and there are many striking illustrations of it In the Azores there are eighteen species of land birds which are permanent residents but there are also several others which reach the islands almost every year after great storms but have never been able to establish themselves In Bermuda the facts are still more striking since there are only ten species of resident birds, while no less than twenty other species of land birds and more than a hundred species of waders and aquatics are frequent visitors often in great numbers but are never able to establish themselves

SUMMARY OF MAMMALIAN DISPERSAL

HANS GADOW

Australia as the earliest great mass of land permanently severed from the rest is in almost undisturbed possession of the lowest mammals It is the sole refuge of the monotremes and the marsupials have narrowly escaped a similar fate They take us to the next independent continent, South America This had three chances or epochs of being stocked with mammals Within the Cretaceous period it seems to have received its marsupial stock from the north the progenitors of all modern marsupials A second influx during the early Tertiary brought edentates and rodents as its first Placentals from Africa and those queer Ungulates the Toxodonts and Pyrotheria unless we prefer to look upon these Eocene extinct orders as truly aboriginal to South America when this was still continuous with the ancient Brazil Afro-Indian Gondwanaland The third and last inroad came once more from the north, when with the close of the Miocene permanent connection with North America was re established This brought the modern odd toed and pair toed Ungulates with dogs cats and bears in their wake and lastly man

There remains the huge North World Eurasia and North America have always formed a wide circumpolar ring which repeatedly broke and joined again Whatever group of terrestrial creatures was developed in the eastern Asiatic half was sure to turn up in the western and vice versa

Lastly the mysterious African continent It began originally as the centre of the ancient equatorial South World it has lost these connections and has become joined to the northland after many vicissitudes It is therefore most difficult to apportion its fauna rightly moreover for fossils it is almost a blank except Egypt. It must have had some share in the evolution of mammals like edentates rodents insectivores hyrax elephants sirenians and lemurs all groups with an ancient stamp But what share it had against Eurasia in the development of say ungulates carnivores monkeys we do not know Not much is likely to have originated in Europe the elephants rhinos hippos lions and hyaenas were migrants rather from than to Africa rarely across some Mediterranean bridge usually by Asia Minor

The more dominant forms of our present fauna have originated to use an expression of Darwin s in the larger areas and more efficient

From Hans Gadow *Wanderings of Animals* (1913) Cambridge University Press.

workshops of the north," and the balance is in favour of Asia as the cradle of modern mammals

Is it an idle dream to think of the future? A survey of the past reveals the vanishing of whole faunas from extensive countries, which were then repeopled by other forms from elsewhere What has happened before may happen in times to come Countless groups once flourishing are no more many others have had their day and are now on the decline whilst others are flourishing now are even in the increase and seem to have a future before them Such favoured assemblies are the toads and frogs lizards and snakes, Passerine birds and rodents mostly the small sized members of their tribes, the days of giants are past All this has happened in the natural course of events without the influence of man who only within most recent times has become the most potent and destructive factor to the ancient faunas of the world

SUMMARY OF THE ARGUMENT FOR EVOLUTION AS BASED ON GEOGRAPHIC DISTRIBUTION

On the hypothesis of special creation or on any other hypothesis except evolution that has even been suggested the extremely intricate patchwork of animal and plant distribution remains an unsolvable picture puzzle without rhyme or reason When this puzzle is attacked with the aid of the evolutionary idea the key to the whole maze is furnished and the difficulties clear up with remarkable ease The whole hodgepodge makes sense and we can understand many previously irreconcilable facts In no field does the working hypothesis of evolution work to such advantage as in this field

On the basis that a species arises at one place spreads out over large areas becoming modified as it goes that new species are formed from old through modification after isolation from the parent stock how do the facts of distribution look when examined in detail?

1 Cosmopolitan groups those with the widest distribution, are those to whom no barriers are sufficient to check migration e g, strong fliers Man earthworms carried by Man

2 Restricted groups are usually those to which barriers are readily set up and are frequently the last remnants of a formerly successful fauna or flora which continue to survive only in some restricted area where the conditions are rather more favorable than elsewhere

3 The study of the distribution of species belonging to a single genus reveals that the more primitive or generalized species occupy a central position and the most specialized species are at the outer boundaries of the distributional area

4 The faunas and floras of continental islands are just what we should expect on the basis that there was at one time a land connection with the nearest continent that at this time the faunas and floras were the same on both island and continent, that later the continent and island were separated by an impassable barrier of ocean and that the inhabitants of the two bodies evolved separately

5 The faunas and floras of oceanic islands are like those of the nearest mainland and are of those types for the most part that might most readily have been blown there by the wind or carried on floating debris

6 The conclusions arrived at by students of geographic distribution, past and present as to the existence of former land connections now broken are borne out by the independent findings of geologists and geographers

PART III

THE MECHANISM OF EVOLUTION (GENETICS)

CHAPTER XIII

INTRODUCTORY STATEMENT

THE NATURE AND SCOPE OF GENETICS

The validity of the general principle of evolution rests on the kind of evidence presented in previous chapters. Volumes could be written giving further evidence of the same sort. Very few thoughtful persons, once confronted with these evidences, fail to be convinced as to the reality of evolution.

It is one thing to know that evolution has occurred and has followed certain courses, but quite another thing to understand what forces underly the process. A going process must have causes, and it is our purpose in this section of the course to present an account of what we know, or what we think we know, about the causes of organic evolution.

Our method of study is one that depends on the validity of the doctrine of uniformitarianism. Exactly as in the science of geology the method of investigation is that of studying in detail the changes going on today, of assuming that present changes are of the same nature as changes in the past, and that the past may be interpreted in terms of what we discover about the present. Thus long series of generations of rapidly breeding animals and plants are studied intensively over periods of years, some species having been bred for over twenty-five years, or for at least seven hundred generations, a period equivalent in number of generations to 25,000 years of human life. Hundreds of millions of individuals have been passed in review before the keenly trained eyes of an army of competent investigators, all on the lookout for the slightest change from the normal. Any observed change is then followed through subsequent generations to determine whether it is hereditary and how it affects the success of individuals possessing it. Studies of this sort, together with examinations of the germ cells to see whether or not correlated changes have occurred in their materials, and mathematical calculations of the relative frequencies with which different characters occur in combination with one another, have led to an understanding of the mechanism of evolution far more complete and detailed than anyone a decade or so ago could possibly have hoped to attain.

The experimental and analytical study of the processes and mech

anisms of evolution is the province of that branch of evolutionary biology known as *Genetics*

Three principal methods of attack upon the problems of genetics are as follows

a) **Experimental breeding** —This method first carried out systematically by Mendel consists of breeding together two individuals differing in certain well defined characters and of determining the ratios in which the contrasting parental characters reappear in successive generations of descendants Mendel s method has been extremely fruitful and in connection with the second method that of cytology has thrown a flood of light on the actual workings of the mechanisms of evolution

b) **Cytology** —This method involves the microscopic study of the germ cells especially during the period of reproduction The observed changes that go on in connection with sexual reproduction have been found to constitute a mechanism adequate to explain the peculiar hereditary regularities constituting Mendel s laws of heredity Also it has been found that most aberrations in heredity are associated with correlated aberrations in the mechanism of reproduction Experimental breeding and cytology have been most intimate and successful collaborators

c) **Statistical analysis** —While experimental breeding and cytology lay stress upon the type of change or the mode of heredity in individuals statistical methods deal chiefly with group changes and with the characteristics of populations Often evolutionary trends or group changes quite undetectable in separate individuals can be detected by statistical methods Al o the statistical consequences of a certain type of change in a few or many individuals can be predicted for any given number of generations While the methods of statistical analysis are as a rule too difficult for any but the expert they are becoming more and more essential as a part of the technique of genetics

d) **Observations of changes going on in nature** —Attempts are made to discover evidences of changes in nature equivalent to those observed in the laboratory and there is now considerable evidence favoring the conclusion that laboratory observations are reliable criteria of what takes place in nature

PREREQUISITES FOR THE STUDY OF GENETICS

In order profitably to pursue the study of genetics one must first understand the fundamentals of biology in general for the mechanism

of evolution is largely within the living organism itself One must be familiar with the units of life cells organisms, generations One must understand the methods of reproduction and the mechanisms of heredity and variation resident in the cellular components of the organism Also one must never forget that organisms live and grow and reproduce only if in an appropriate environment and that the environment has much to do with the expression of hereditary characters In addition, the environment acts as a guiding factor directing the course of evolution along lines of fitness or adaption The highly varied character of the environment, moreover tends to favor a high degree of diversity in organisms and thus to give rise to a vast multiplicity of different types

In view of all this it will be necessary for the general student who has had no previous training in biology to learn the fundamentals of this subject before proceeding with the more specific materials of genetics

THE MECHANISM OF EVOLUTION

At the beginning of the present century very little was known about the actual mechanism of evolution We had Darwin s theory of natural selection Weismann s theory of germinal continuity and a statistical knowledge of certain aspects of variation and heredity Something was known about the rôle of isolation in species-forming and the general fact of orthogenesis was appreciated With the rediscovery in 1900 of Mendel s work and the announcement by De Vries of the mutation theory genetics really began Thirty odd years of intensive research by hundreds of specialists have contributed so much to our understanding of the workings of evolution that we now consider that we know something about the main causes of evolution

Evolution is now looked upon as an extremely complicated process There is no one cause of evolution as the extreme proponents of natural election once held rather there are many causes each acting upon and in co-ordination with all the others The mechanism of evolution is like an intricate piece of machinery manufacturing a complex product Each part is geared up with other parts Some parts are concerned with feeding in the raw materials others with separating and distributing the raw materials others with assembling and shaping up the various parts into something useful and with discarding defective and useless parts and still others with sorting out the different kinds of products and keeping them in separate lots

No man made mechanism is so intricate as is the mechanism of evolution, for all man made machines are designed to turn out uniform products while the evolution machine is especially adapted to turn out highly diverse products

Although we recognize that none of the causal factors of evolution are independent it makes for clearness of exposition to subdivide the complex machine into five separate factors, each in itself complex enough for further subdivision

THE MAIN CAUSAL FACTORS OF EVOLUTION

I **Persistence factors** —Under this head are included all agents that make for persistence of type in organisms resulting in relative constancy of form and function over long periods of time When characters persist unchanged from generation to generation, they are said to be hereditary It is part of our plan to find out what parts of the mechanism promote constancy of type Some of the principal reasons for this constancy are the following

a) The relative stability of the unit materials of heredity, the *genes*
b) The relative constancy of bundles of genes the *chromosomes*
c) The relative constancy and perfection of operation of the mechanism of *mitotic cell division* a mechanism that aids in maintaining the constancy of (*a*) and (*b*)
d) The relative constancy of the principal factors of the environment over long periods of time

II **Diversity factors** — Diversity may be defined as variety without the introduction of anything definitely new It involves first the kaleidoscopic recombination of all the various hereditary unit characters without any change in the unit characters themselves and second the almost equally varied expression of characters under the influence of a highly variable and diversified environment

The chief agent in promoting diversity of combinations is sexual or gametic reproduction And the specific mechanisms involved are the mechanisms of *meiosis* and *fertilization*, which are later to be described in detail

The recombinations of unit characters while apparently random in individual cases, give constant statistical ratios that are known as 'Mendelian ratios Mendel s Laws of heredity in general are in fact the laws of the random assortment and recombination of unit characters through the instrumentality of meiosis and fertilization

Much of the endless diversity of living beings is however not hereditary at all but is due to variations in the environment The differences in the sizes of beans on a single bean plant for example are purely environmental in origin, as experiments have shown and not in the least hereditary

III Change factors —Change in contrast with diversity involves the introduction of new unit characters or new gene arrangements It is as though a new piece of colored glass were added to those already present in the kaleidoscope or a piece of a different color substituted for an old piece thus changing all future patterns Such changes result from the rare modification of individual genes from equally rare changes in the number of chromosomes and from the shifting of groups of genes within a chromosome or from one chromosome to another The mechanisms involved are

- *a*) Gene mutations
- *b*) Slips in the regularity of mitosis involving irregularities in the relatively constant operations of heredity The result is a change in the number of chromosomes Several kinds of such irregularities are known and all are called *chromosomal aberrations*
- *c*) Breaks in chromosomes followed by the reunion of the broken pieces in various new arrangements Such changes are known as *translocations*
- *d*) While most of the changes under (*a*) (*b*) and (*c*) seem to occur spontaneously there is some evidence that they may have environmental causes Hence the environment may be the ultimate change factor

IV Guiding factors —Evolution has been for the most part orderly especially in two respects (*a*) The best known fossil pedigrees indicate that changes from age to age tend to follow certain definite trends We have previously spoken of this phenomenon as *orthogenesis* (*b*) Evolutionary changes have also been at least to a large extent *adaptive* Most changes have been appropriate to changes in the environment

The chief guiding factor commonly held responsible for both orthogenesis and adaptation is *natural selection* a causal factor of great importance that will be discussed critically in its proper place

Various mystical guiding factors such as Driesch s *enteleche* and Bergson s *elan vital* have been posited to account for the apparent

purposiveness of evolution but there is little evidence for the existence of such factors

Lamarck's theory of the *inheritance of acquired characters* was also designed to explain the adaptive character of evolutionary change but there are many reasons for doubting the validity of this theory

V Dividing factors —One of the most striking features of living organisms is their multiplicity of different kinds phyla classes orders, families genera species and varieties Evolution has involved the subdividing of old types into numbers of new ones The whole process has been one of the branching out into numerous diverging lines of descent All those agencies that promote the splitting of all old species into two or more new ones are classed as isolation factors There are many means of isolating portions of a species from other portions of the same species These may for convenience be called

a) Geographic isolation
b) Reproductive isolation
c) Psychic isolation
d) Environmental isolation

In general any agent that prevents a particular variant of a species from breeding with the more typical members of that species tends to help to establish the variant type and aids in the production of a distinct new variety species or genus depending on the degree of completeness of isolation and the length of time involved

All of these factors are necessary agents in bringing about the kind of evolution that we know has occurred With perfect heredity and no diversity or change factors the organic world would be at a stand still Successive generations would be exact duplicates of one another Offspring would be exactly like their parents and no evolution would be possible The diversity and change factors without the conserving factor heredity would produce nothing but chaos Two successive generations would be utterly unrelated offspring would be nothing like their parents and change would merely run riot With the heredity diversity and change mechanisms operating as they are known to do but without any guiding factor living things would be little more than a chaotic collection of monstrosities unfit and ill assorted With all the other factors operating as they are known to do but with no dividing factor evolution would proceed along but one front line of advance There would be no multiplicity of groups no system of

branching relationships Thus it is obvious that the factors of evolution are to be conceived of not as independent mechanisms but as interdependent parts of one grand mechanism

It is our purpose to discuss in detail the various component factors of the mechanism of evolution approximately in the order in which they have been listed in this outline

CHAPTER XIV

THE BIOLOGICAL BACKGROUND OF GENETICS

RACES AND INDIVIDUALS

Evolution is racial change In order that a race may change the individuals comprising the race mu t in large numbers exhibit changed conditions One or a few individuals changing in some peculiar way may not at all affect the status of the species as a whole It is well then to remember that true evolutionary changes are mass changes involving whole populations through successive generations A race or a species is to be looked upon as a vast unit continuous in time and space The members of a race are all descended from common ancestors and are interbreeding in all sorts of ways If one should work out a diagram of the genetic relationships of the members of a large species such a diagram of connecting lines of relationship would constitute an almost solid mass of interlacing lines An intricately interconnected group of individuals constituting a race is then a true evolutionary unit Just as cells are the structural units of life so races are the *evolutionary units* of life Let us now briefly examine the constitution of a race

At any given period of time a race consists of a large group of individuals Some of these are related as parents and offspring others as brothers and sisters others as cousins of varying grades and all doubtless trace back to some common ancestors a score of generations ago The individuals constituting the race at one period are not at all the same individuals that constituted that race a few years previously and none of them will be represented in that race a few years hence Individuals then are temporary components of the race, but the race itself is permanent and relatively constant, though slowly changing as a whole

It is our problem to determine the relation of the individual to the race and to account for both the relative constancy and the slow change of the race made up as it is of such mortal units as individuals More specifically we must study the make up of the individual and learn how replacements are made when individuals wear out

THE CELLULAR MAKE UP OF INDIVIDUALS

All living things except possibly the filterable viruses and bacteriophages are made up of vital units known as *cells* Many of the

lower organisms are unicellular, but all of the higher organisms are multicellular

A complex organism such as a man or an insect consists of millions of cells Each cell bears a life of its own but is dependent for its supplies of food and oxygen upon other cells and in turn performs some function that is of value to the organism as a whole The division of labor and interdependence of the innumerable cells of the cell republic the organism is reflected in the fact that groups of cells of a particular sort constitute tissues that various combinations of tissues form organs, and that various combinations of organs form systems such as the nervous system the digestive system the circulatory system and others No matter how elaborate the specialization of organs and systems may be every living part is composed of cells Cells are perhaps the most fundamental units of life in about the same sense that atoms are the fundamental units of matter itself Also cells possess certain mechanisms which are the principal agents both in preserving constancy of form and function (heredity) and in promoting diversity and change (variation) Hence if we desire to understand how evolution takes place, it behooves us to make a careful examination of the constitution of cells

A TYPICAL CELL AND ITS COMPONENT PARTS

Cells vary in size and in form according to the special functions they subserve but in spite of their numerous specializations they have many features in common The diagram of a cell shown in Figure 40 is not meant to represent any particular kind of cell but is a composite of many kinds of cells Of course no one kind of cell contains all of the cell organs shown in this diagram

The two most important subdivisions of the cell are the nucleus and the cytosome or cytoplasm

The nucleus is a more or less centrally situated body commonly spherical in form and separated most of the time from the cytosome by a *nuclear membrane* Within the nucleus is a characteristic material known as *chromatin* which at times condenses into definite bodies known as *chromosomes* each chromosome consisting of a bundle of *genes* or hereditary units

The cytosome consists of all the rest of the cell except the nucleus All the vast hordes of cells of different sorts constituting a given complex organism are identical in their nuclei but in any cell the cytoplasm differs in its form and structure according to its location in the

organism and its special function Thus a nerve cell and a muscle cell of a given organism may be utterly different in general form and function but the nuclei of both are the same Since the specific hereditary materials of the individual are possessed equally by all of the cells of that individual it follows that the differences in cells and tissues must be solely cytoplasmic How these differences arise is a problem

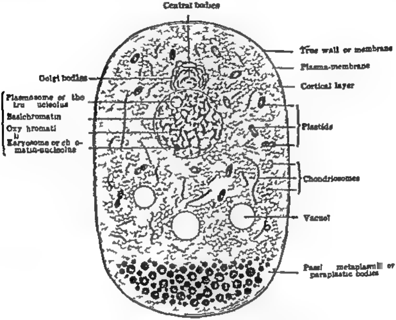

FIG 40 —Diagram of a typical cell Its cytoplasmic basis is shown as a granular meshwork or framework in which are suspended various differentiated granules fabrillae and other formed components (*From E B Wilson*)

of individual development rather than one of racial evolution Many of the slow and steady trends in evolution however, are believed by some authorities to be the result of general hereditary changes in the cytoplasm but there is a great deal of evidence favoring the conclusion that the nucleus is the chief organ of heredity and of variation in the cell

Details of the nucleus —The nucleus except during the process of mitotic cell division is surrounded by a definite membrane the *nuclear membrane* which separates the clear *nuclear sap* from the cytoplasm outside the nucleus During the resting stage between two cell divisions there is a network of *linin* fibers running throughout the nucleus

Upon this linin network are strung numerous granules of a deeply staining substance, or substances called *chromatin granules* Other nuclear bodies known as *nucleoli plasmosomes* and *karyosomes* are found in some nuclei but they may be ignored so far as our knowledge of their rôle in evolution is concerned

Chromosomes —Far more important for our purposes than any other cellular components are the *chromosomes* Preparatory to the process of mitosis the diffusely scattered granules of chromatin condense into semi solid masses sometimes spherical or ovoid sometime rodlike, sometimes V shaped etc These are the chromosomes Each species of organism possesses in all its cells a certain definite number and kind of chromosomes Man has 48 *Drosophila melanogaster* has 8 *Oenothera lamarckiana* has 14, *Ascaris megalocephala* has 4 in one variety and 2 in another, some crustaceans and some roses have over a hundred chromosomes Careful studies of the chromosomes of numerous species of both animals and plants have revealed the significant fact that except in the males of some species the numbers of chromosomes are *even* Furthermore it is possible to match them up in pairs according to their sizes and shapes The significance of this becomes clear when we remember the fact that an individual starts out from a *ygote* (fertilized egg) which is a composite cell to which each parent has contributed one full set of chromosomes

Genes —At this time it seems well to anticipate the later results of genetic research to the extent of stating that each kind of chromosome contains a unique series of hereditary units (genes) Certain genes lie in certain chromosomes and all the genes in a particular chromosome are probably arranged in linear order like beads on a string Since the orderly arrangement of genes in bundles (chromosomes) and their specific arrangement within a given bundle are both important in heredity it is essential that this specific organization be maintained during development and reproduction *It is also essential for persistence of type from generation to generation that the complete organization not only of nucleus but of the cytosome, be maintained* This is accomplished by that heredity mechanism par excellence the *mechanism of mitosis*

The central body —Imbedded in the cytoplasm usually in close proximity to the nuclear membrane lies a structure known as the *central body (centrosome)* In most animal cells this structure is well defined but it is absent in most plant cells The central body is primarily associated with cell division as will be seen later

CELL DIVISION—MITOSIS

Each cell during periods of growth and development grows to a definite size and then divides into two daughter cells Repeated cell divisions multiply vastly the numbers of cells in a developing embryo, until in higher organisms millions of cells are produced To make what might easily be a long story as short as possible let it be sufficient to state that the chief features of mitotic cell division (mitosis) are as follows The central body divides and the two centers migrate apart spinning between them a spindle of fibers the *mitotic spindle* (Fig 41) The nuclear membrane disappears, and as the two central bodies migrate farther and farther apart the chromosomes which have in the meantime gradually become more and more compact, move toward the equator of the spindle, each attached by two fibers probably composed of linin one fiber leading to one pole of the spindle, the other fiber to the other pole (Fig 4) Usually even before migrating into the spindle each chromosome has become a double body a pair of joined twins each one the exact duplicate from end to end of the other Each gene in the gene chain has previously twinned so that each gene in each chromosome is a double or twin gene The chromosomes now arrange themselves in a plane at right angles to the long axis of the spindle each chromosome having one of its twin halves directed to one pole and the other to the opposite pole All of the stages up to this point of equilibrium are known as *prophases* of mitosis the equilibrium phase being the *metaphase* (Fig 42 E)

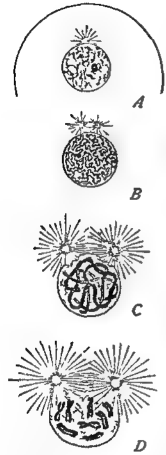

FIG 41 —Diagram of the early phases of mitosis in *Ascaris* A vegetative nucleus B fine spireme C coarse spireme D late prophase with chromosomes spindles forming (*From E B Wilson*)

Now the real separation phase of division begins The twin components of each chromosome seem to be pulled apart possibly by the fibers attached to them and one twin migrates to one pole the other twin to the other (Fig 43 *H*) Slowly the various chromosome twins approach opposite poles and finally cluster closely about the latter At this point the cell wall constricts at the equator and soon divides the single cell into twin daughter cells (Fig 43 *I*) Not only are the chromosomes divided meticulously into equal lots but all the cytoplasmic parts of the cell are so divided that each daughter cell comes to have exactly the same detailed organization as had the mother cell from which they were derived The period during which chromosome halves migrate to the poles of the spindle is called the *anaphase* while that during which the chromosomes lose their density and reform the chromatin network with which we started is called the *telophase*

By means of this elaborate routine of division the exact specific organization of the cell is maintained at least in the *germ track* In this process of mitosis we have a view of the mechanics of heredity which if uninterrupted would maintain perfect constancy of type for all time unless a new order of environment were to alter the expression of a fixed hereditary complex or some other mechanism promoting diversity were to intervene

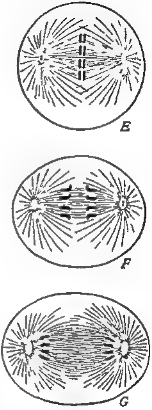

FIG 43 —Diagram of the middle phases of mitosis *E* metaphase *F G* earlier and later anaphases (*From Wilson*)

DIFFERENTIATION

Not merely do cells multiply in the process of embryonic development but at every step differentiation of cell for the performance of different specialized functions is going on The mechanism of differentiation is at present very incompletely understood and what we do know is of a technical nature and difficult to present without a back

ground of embryological lore In very brief, it must suffice for present purposes to state that differentiation is accomplished partially by unequal cell division, in which the two daughter cells come to possess different cytoplasmic contents partially by the differences in position of cells with respect to the environment partially by differences in the relations of certain cells to other cells that have already assumed special characters owing to their original position or their special relation to the environment, and partially by the fact that certain genes are effective only at a given time in development or when cells are in a certain physiological state All cells in an organism are believed to possess the same genes but particular genes become effective only under special conditions of time and place Some such complex of intricate interrelations at present very obscure even to the most advanced students of embryology seems to underly cellular differentiation While the geneticist cannot avoid all responsibility for the solution of these insistent problems he may with some appropriateness delegate them for the present at least, to the experimental embryologist At any rate, it seems best at the present juncture to sidestep the problems of differentiation and to get back on surer ground more familiar to geneticists and more applicable to their problems

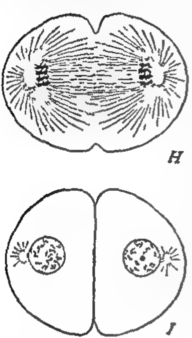

FIG 43 —Diagram of the end phases of mitosis *H* the beginning of constriction of the cell membrane *I* the completed division (*From Wilson*)

THE ORIGIN OF NEW INDIVIDUALS

MODES OF REPRODUCTION

Since individuals the temporary components of the race or species are continually running their courses and dying off replacements are necessary if the race is to persist The replacement of old individuals by new is commonly called *reproduction* There are numerous modes

of reproduction, but they may all be classified into two main categories *somatogenic* and *cytogenic* Somatogenic reproduction is accomplished without the instrumentality of sex and involves the subdivision of the parent body into two or many fragments each of which has the power to reconstitute a whole new individual like the parent In unicellular organisms somatogenic reproduction involves the division of the one celled body into two or more cells each capable of growing into a full sized individual, in multicellular organisms the products of division are multicellular fragments Cytogenic reproduction is accomplished by means of unicellular germ cells which must pass through processes of growth and division in order to reconstitute the multicellular body typical of the species to which they belong

The essential feature of all reproductive processes is that some portion of the parent is isolated or physically cut off from the parent s body, an integral part of which it formerly was On ceasing to be a part of an organized system it exercises its prerogative of developing a system of its own in the image of the one from which it was derived This is true whether the isolated part be a single cell or a multicellular fragment This is perhaps to be expected in view of the fact that each cell possesses the hereditary organization characteristic of the race or species

Varieties of somatogenic reproduction—In *unicellular organisms* the principal modes of sexless reproduction are transverse fission in which the division is across the long axis of the cell longitudinal fission, in which the division is parallel with the long axis and multiple fission in which the nucleus divides several times before the cytoplasm partitions the several nuclei off to form separate cells In *multicellular organisms* the principle modes of somatogenic reproduction correspond rather closely to those among unicellulars but several special modes are added *Transverse fission* is common among worms of various kinds and among the larvae of certain jelly fishes *Longitudinal fission* takes place in the early embryos of a number of mammals as in armadillos and in man resulting in true quadruplets and true twins derived from an original single embryo *Multiple fission* occurs in a number of parasitic insects in which the multicellular embryo subdivides into hundreds of cell masses each of which becomes a complete individual In addition to these types of fission multicellular organisms reproduce by *budding* which may be simple or multiple Budding involves the outgrowth of a minor portion of the parent body the latter body being left intact—this being in contrast with

fission processes in which the entire parent body is distributed among the progeny *Gemmulation* is a peculiar form of somatogenic repro duction found among sponges involving the gathering together of samples of all the various kinds of cells into compact little balls called *gemmules* which survive the dead parent and escape to form new sponges when the parent body disintegrates

Artificial propagation of both plants and animals is made possible through the ability of many organisms to regenerate a whole new in dividual from a small part of a parent organism Thus sponges may be cut up into minute fragments and distributed like seeds upon a slab of concrete each fragment growing up into a sponge of the parental type Everyone is familiar with the fact that gardeners propagate many plants by planting cuttings and that potato tubers (enlarged parts of the underground stem) may be cut into as many fragments as there are eyes and that each will produce a plant with tubers like the parental tuber

All the cells involved in somatogenic reproduction are the product of ordinary mitotic division which maintains so painstakingly the hereditary organization of the species No wonder, then that this mode of reproduction makes for a high degree of constancy of type Apart from the effects of differences in the environment which appear not to be inherited there is nothing about somatogenic reproduction to favor diversity or change If one desires to study pure heredity uncomplicated by sex and its diversifying effects one should study successive generations produced by somatogenic reproduction

Varieties of cytogenic reproduction —All those forms of reproduc tion in which single cells become separated from parent bodies to give rise to new individuals fall into this category The first and simplest form of cytogenic reproduction is *spore formation* Among plants reproduction by spores is well nigh universal though many also make use of gametes A spore is nothing more than a small cell produced by mitosis from previous cells Spores are commonly motile some being furnished with flagella by means of which they travel through the water others being so light as to be wind borne To reproduce a new organism a spore after a period of rest, merely divides and redivides and thus forms a new multicellular body

In some of the lower plants motile spores all visibly similar, swim about actively in swarms and then pair off two by two and fuse to form *zygotes* from which new plants develop These mating cells are called *gametes* This is the most primitive expression of sex in plants

Further specialization of sex cells involves, first, the differentiation of gametes into large passive gametes (*eggs*) and small motile gametes (*sperms*) and second the differentiation of sex individuals *males* and *females*

At this point it is important to emphasize the fact that sex although it appears to be so intimately associated with reproduction is in no way essential to reproduction In fact it is a hindrance rather than a help to the mere multiplication of individuals Sex is a mechanism that has been superimposed upon reproduction and has a function only remotely associated with the latter In a word sex is the *diversity mechanism* with which we shall deal fully at the proper time

The *female gamete* or *egg* is always relatively large Even the tiniest of eggs such as those of placental mammals are relatively large as compared with tissue cells The human egg (ovum) for example has a cubic content of about a thousand times that of the average tissue cell while the eggs of birds and sharks are thousands of times bulkier than mammalian eggs This great increase in the size of eggs is due largely to the accumulation of food material (yolk) that serves to sustain the embryo and give it a good start in life Most eggs are when full grown spherical or ovoid in form and most of them are protected by envelopes of one kind or another

Male gametes or *sperms* are highly variable in shape and are relatively extremely small and active Most of the cytoplasm of the sperm is specialized for locomotor purposes Some sperms have one long tail like a snake (Fig 47 *f*) others have two or several tails and still others have numerous radiating locomotor processes resembling the thorns of a sand burr In general a sperm gives the impression of being a highly specialized cell one of whose main functions is that of finding and penetrating the egg Sperms are thousands sometimes millions of times as numerous as eggs thus making it more probable that at least one sperm will reach each mature egg

When the sperm approaches the egg it seems to be guided at least in some cases by a specific chemical substance given off by the egg When egg and sperm meet the latter penetrates the former more or less completely (Fig 50 *a*) Sometimes the whole sperm enters the egg sometimes only the head of the sperm containing the nucleus and a minute amount of cytoplasm On entering the egg cytoplasm the sperm nucleus grows at the expense of the latter and becomes nearly or quite as large as the egg nucleus (Fig 50 *c d e*) The union of egg and sperm is called *fertilization* and the product of the union is a *zygote*

The term "zygote is also sometimes used to designate the organism that develops from the united gametes

Gametic reproduction is very frequently evaded in both animals and plants by the use of a process known as *parthenogenesis* or 'virgin birth' in which eggs develop without any aid from sperms Some instances of this peculiar aberration of gametic reproduction will be discussed in a special chapter on the biology of sex (chap xvii) Here we have the anomalous situation of gametic (or marrying) reproduction without the presence of both sexes Long-continued parthogenesis involves the reduction of diversity and results in constancy as marked as that which is associated with various forms of sexless reproduction

While the great majority of animals and plants are sexually dimorphic consisting of male individuals that produce sperms and female individuals that produce eggs large numbers of both animals and plants are *monoecious* having both sexes present in one individual Such forms among animals are known as *hermaphrodites* In some hermaphrodites eggs are fertilized by own sperms in others mating occurs in which a mutual exchange of sperms takes place In the latter instances the advantages of sex in enhancing diversity are retained and mating is facilitated because any two adult individuals may mate but in the former instances where self fertilization occurs, diversity is reduced to the level found among organisms reproducing by asexual methods It is possible therefore to produce from such self fertilizing monoecious species *pure lines* in which all progeny of a single individual are genetically identical In a later connection we shall make use of such forms as these to study heredity in its simplest expression (chap xv)

THE ORIGIN OF GAMETES

Two important questions arise in connection with gametes (*a*) From what cells in the parent body do gametes arise? (*b*) What changes occur in germ cells that make it possible for them to unite in pairs to form zygotes?

The germ track —The question as to whether germ cells are derived from parental tissues that have been more or less specialized for other functions, or whether they are derived from an unbroken series of germ cells set apart from bodily functioning at all times is one of great importance for theories of heredity The prevailing view of biologists is that at least in the higher animals and possibly in all animals and plants the germ cells are produced from cells that have never in any

generation gone through a period of specialization for any particular bodily function In animals these cells are believed to be set apart early in ontogeny (the development of the individual) and localized in *sex glands* or *gonads* In plants the germ track is believed to be maintained in the meristematic cells of growing points but germ cells are not so definitely localized as in most animals

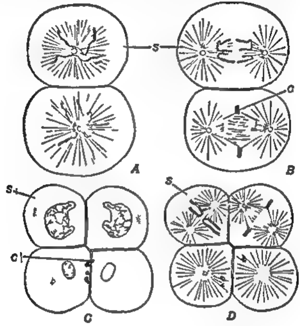

FIG 44—The germ track in *Ascaris* Stages in early cleavage showing the chromatin diminution proces in all cells except the stem cell (*S*) (*From Bo ers 189 *)

In some animals the germ track is very clear and unmistakable from the beginning of one generation to that of the next The classic instances of germinal continuity are those of the roundworm *Ascaris megalocephala* and the fly *Miastor americana*

In the variety of *Ascaris* known as *uni alens* which possesses only two chromosomes to each cell (incidentally the lowest number known) the developmental stages are as follows at the first division of the zygote two cells are formed in the usual way each cell with two long loop-like chromosomes (Fig 44 *A*) One of these two cells however undergoes a striking nuclear change involving the breaking off of the

ends of the chromosomes and the disintegration into small chromatin granules of the middle portions The large ends of the chromosomes are discarded into the cytoplasm and absorbed, while the smaller granules are all that the descendants of this cell have for chromosomes It is significant that the progeny of such cells form only body cells in this case skin and nerve cells (Fig 44 A) The other cell remains just like the original zygote and is a stem cell or germ cell This cell then divides and one of the daughter cells retains the full germinal character while the other breaks down its chromosomes as before and gives rise to tissues that line the digestive tract (Fig 44 B) Once more the germ cell divides and one of its daughter cells undergoes chromosome breakdown its cell progeny forming chiefly such tissues as muscles blood vessels and connective tissues (Fig 44 D) From this point on the germ cells are definitely set apart and contribute no further to the soma They give rise to nothing but germ cells and ultimately to gametes The unbroken series of cells with intact chromosomes from the zygote to gametes is the *germ track* and the chromosomes of these cells carry the so called *germ plasm* The rest of the embryo constitutes the *soma* or *somatoplasm* The relation of body to germ plasm is well shown in the accompanying diagram (Fig 45)

A second example of a well defined germ track is found in *Miastor* (Fig 46 A) in which a single definite germ cell (*p g c*) is set aside at the very first division of the zygote The other cell divides repeatedly, casting out parts of the chromosomes as in *Ascaris*, and ultimately giving rise to all the soma Even in a fairly advanced embryo (Fig 46 B) the large germ cells are clearly seen in a small group (*oog*$_1$) These give rise ultimately to the gametes

While in vertebrates the germ track is ill defined and difficult to follow there seems to be no doubt that it exists Some investigators however claim that the original primordial germ cells disintegrate and come to naught and that the gametes arise from a new lot of germ cells that are derived afresh from generalized epithelium If that be the case it seems fair to consider this epithelium as part of the germ track and not as a differentiated part of the soma At least it may be said with confidence that in none of the higher mammals are germ cells ever derived from specialized body cells such as muscle cells nerve cells or gland cells Our question as to the origin of the germ cells seems to be answered They are derived in an unbroken series from previous germ cells by the process of mitosis This is the basis of Weismann s concept of *the continuity of the germ plasm*

THE MATURING OF GAMETES

The primordial germ cells, previously described as having been set apart from the soma at a relatively early period of development and located in germ glands (*ovaries* and *testes*) pass through a period of comparative inactivity until sexual maturity arrives At the dawn

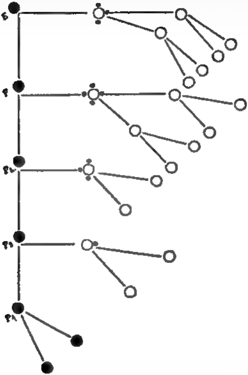

Fig 45 —Diagram of the germ track in *Ascaris* E egg P P P_3 stem (germinal) cells P_4 primordial germ cell Circles represent somatic cells while the four black dots outside of the circles represent the masses of chromatin that are eliminated (*From Boveri 1910*)

of sexual maturity the germ cells wake up and enter upon a period of great activity, during which mature gametes are produced The history of the production of gametes differs somewhat in the two sexes That of the male called *spermatogenesis* is a little simpler than that of the female called *oogenesis* and will be described first

Spermatogenesis —The first sign of renewed activity of the male germ cells is evidenced by a succession of rapid cell divisions the

mechanism of mitosis being used After many thousands of germ cells have been produced multiplication is stopped and growth sets in, the growth in the male cells being very slight as compared with that of female cells During the period of growth the chromosomes not only split to form twin chromosomes, as though in preparation for mitosis, but whole homologous chromosomes unite in pairs, a process known

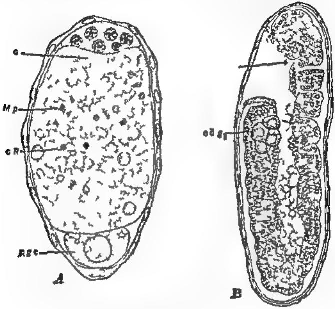

Fig 46 —The germ track in *Miastor americana* *A* germ-cell (*p g c*) set apart in the eight-celled stage of cleavage (*After Hegner*) The walls of the remaining seven somatic cells have not yet formed though the resting or the dividing (*M p*) nuclei may be seen *C R* chromatin fragments cast off from the somatic cells *B* section lengthwise of a later embryo of *Miastor* the primordial egg-cells (*oog*) are conspicuous (*From Guyer after Hegner*)

as *synapsis* The result is that instead of the set of single chromosomes characteristic of the zygote there are groups of four (*tetrads*) each tetrad composed of two pairs of twin chromosomes bound together There are just half as many tetrads as there are chromosomes in the zygote Now follow two special cell divisions known as *meiosis*, without any further change in the chromosomes The result is that one chromosome of each tetrad goes to each of the four matured sperm cells In one of these divisions the so-called *reduction division* both twins of an originally single chromosome pass together to one cell

which results in a reduction of the number of chromosomes characteristic of the zygote to one half (Fig 47) The other division simply separates twin chromosomes as in ordinary mitosis The result is that each gamete has only one of each kind of chromosome and therefore only one half the number possessed by the zygote and the primordial germ cells It is customary to speak of the somatic or zygotic

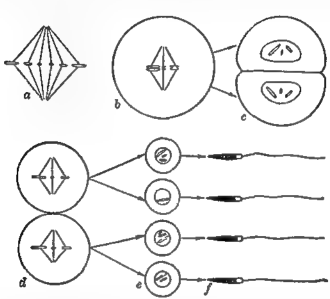

Fig 47 —Diagram to illustrate spermatogenesis *a* showing the diploid number of chromosomes (six is arbitrarily chosen) as they occur in divisions of ordinary cells and spermatogonia *b* the pairing (synapsis) of corresponding mates in the primary spermatocyte preparatory to reduction *c* each secondary spermatocyte receives three the haploid number of chromosomes *d* division of the secondary spermatocytes to form *e* spermatids which transform into *f* spermatozoa (*From Guyer*)

number as *diploid* or *2n* and the gametic number as *haploid* or *n* The final phase of spermatogenesis consists of an elaborate specialization of the male gamete consisting of the development of locomotor organs and adaptations for penetrating the egg

Oogenesis —The period of multiplication is essentially the same as in spermatogenesis except that fewer and larger cells are produced The period of growth is very marked for it is during this period that the egg accumulates the yolk which is usually massed at the vegetal pole The nucleus and central body confined to a small region of

clear protoplasm at the animal pole are not in a position to bring about an equal cell division Hence the maturation divisions are very unequal (Fig 48) The first maturation division results in a large cell not appreciably smaller than the full grown egg and a very tiny cell called the *first polar body* The second maturation division results in a *second polar body* and the mature female gamete or unfertilized egg Sometimes the first polar body divides again, sometimes not Typically however, four female gametes are produced, corresponding in

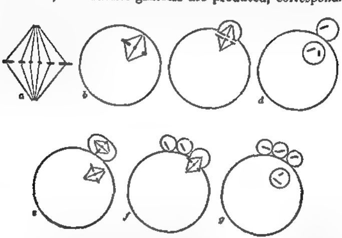

Fig 48—Diagram to illustrate oogenesis *a* showing the diploid number of chromosomes (six is arbitrarily chosen) as they occur in ordinary cells and in oogonia *b* the pairing of corresponding mates preparatory to reduction *c d* the reduction division giving off the first polar body *e* egg preparing to give off the second polar body first polar body ready for division *f* second polar body ready for division *g* second polar body given off division of first polar body completed The egg nucleus now known as the female pronucleus and each polar body contain the reduced or haploid number of chromosomes (*From Guyer*)

number to male gametes similarly produced but three out of every four eggs namely the polar bodies are abortive and die because of deficiency of cytoplasm leaving only the one large well nourished egg as the progeny of each primordial germ cell that completed the period of growth Synapsis and the reduction division are the same in oogenesis as in spermatogenesis (Fig 49)

Now during both spermatogenesis and oogenesis the united pairs of homologous chromosomes one derived from the father and one from the mother of the previous generation arrange themselves during the reduction division quite independently of one another so that some maternal and some paternal chromosomes enter each gamete Where

there are large numbers of chromosomes very many different assortments of maternal and paternal chromosomes are produced This shuffling and dealing of parental heredity materials constitutes one of the principal means of increasing diversity in organisms and therefore one of the most important mechanisms of evolution A relatively

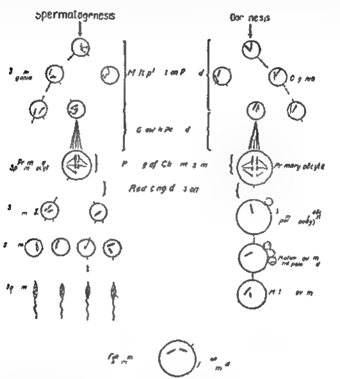

FIG 49—Diagram showing the parallel between maturation of the sperm cell and maturation of the ovum (*From Guyer*)

simple case of the assortment of different chromosomes to gametes is shown in Figure 99

THE UNION OF GAMETES—FERTILIZATION

Once the gametes are mature they are ready for the fertilization process (Fig 50) It seems to be a matter of pure chance that any particular sperm finds and enters any particular egg Since there are usually hundreds of different kinds of eggs and equally large numbers of different kinds of sperms the number of possible kinds of zygotes produced is extremely great If for example a species has only

twenty chromosomes—less than half that possessed by man—there would be $(2)^{10}$, or 1 024 different gametes in each sex And since each kind of egg is as likely to be fertilized by one kind of sperm as another there might be produced $(1024)^2$ or 1 048 576 different zygotes Hence meiosis and fertilization together constitute an extremely effec

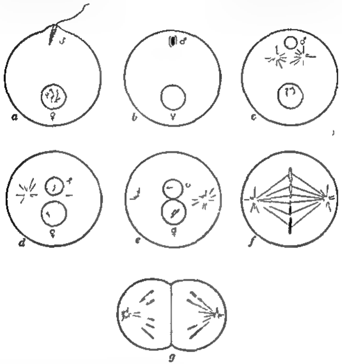

FIG 50 —Diagram to illustrate fertilization ♂ male pronucleus ♀ female pronucleus observe that the chromosomes of maternal and paternal origin respectively do not fuse (*From Guyer*)

tive mechanism for increasing diversity This is the chief rôle played by sex in evolution

This abbreviated account of biological processes is all that is needed for our purpose and should we believe enable the student to follow intelligently the accounts of heredity variation selection and isolation that are to follow A more detailed account of the processes of mitosis, meiosis and fertilization may be found in chapter xliv The Mechanism of Mendelian Heredity'

CHAPTER XV

INTRODUCTION TO THE STUDY OF PERSISTENCE FACTORS

As was pointed out in chapter xiii the principal agents that make for constancy or persistence of type from generation to generation are (a) the relative stability of the units of heredity genes (b) the relative stability of the bundles of genes chromosomes (c) the relative precision and perfection in operation of mitosis (d) the relative constancy of the environment over long periods

Laborious studies of gene changes especially in the fruit fly *Drosophila* have shown that genes are exceedingly stable Muller and Altenberg have discovered that a large proportion of the genes of *Drosophila* must have a stability comparable with that of the atoms of the element radium which have an average unchanged life of about two thousand years Of course where there are hundreds possibly thousands, of genes in each cell the chances of some gene change being observed during any given period will depend upon the numbers of genes present and the number of individuals examined

Chromosomes are probably almost equally stable except for crossing over a phenomenon that cannot be discussed here Changes in numbers and composition of chromosomes do occur as rare accidents of mitosis or meiosis and these changes break up the constancy of cellular organization, but the relative constancy of chromosomal numbers and of their genic content constitutes one of the most important agents in maintaining persistence of types

Various kinds of irregularities in the characteristically constant and nearly perfect mechanism of mitosis are responsible for rare changes in chromosome numbers and for redistribution of genes in chromosomes but these events are so rare that they only very slightly affect the constancy of the species of animals and plants in which they occur

Another factor influencing persistence that is likely to be neglected is that of the relative constancy of the environment in any given geographic region It is well known that apart from seasonal fluctuations the general climatic conditions in a given region remain unchanged over long periods of time The mean annual temperature

the mean annual rainfall and the general character and direction of air movements remain essentially the same for very long periods. Such constancy of environment could hardly fail to exercise a standardizing effect upon animal and plant communities and thus aid in maintaining constancy in the expression of racial characters.

Persistence and diversity mechanisms contrasted.—It is customary in courses in genetics to introduce the study of heredity by presenting an outline of Mendelian heredity. This seems to us a mistake, for Mendelian heredity is really not essentially a persistence factor but rather a most effective diversity factor. It breaks up constancy of combinations of unit characters and promotes multiplicity of recombinations of such characters. For this reason we shall begin our discussion of the persistence factors in evolution with the study of heredity in *pure lines* in which the persistence mechanism is free to operate without being complicated by the diversity mechanism. Since biometric methods are necessary for the study of variation and heredity in pure lines it is necessary to introduce a brief statement about these methods.

A short lesson in biometry.—When character differences are either qualitative or are sharply defined they are easily handled by Mendelian methods. If for example all individuals are either black or white, tall or short heavy or light and no gradations occur between the two alternatives, it is easy to follow the distinct types through successive generations. If on the other hand there occur all gradations between black and white all gradations between tall and short and all gradations between heavy and light it is no longer possible to classify each individual in some particular category. When this is the case the only possible method of finding out how much is inherited and how much is not is to study whole generations of progeny as units and to determine what is the characteristic of one whole generation as compared with the next whole generation. Such a comparison requires statistical methods.

Suppose for example we want to find out whether the size of bean seeds is hereditary or merely environmental we shall have to measure the seeds of the parent and compare them with those of the offspring. There would be nothing gained by comparing a selected seed of the parent with one of the offspring. We must compare the total of one with the total of the other. It is necessary then, to find a method or methods of comparing the parent condition as a whole with the offspring condition as a whole. Some simple method must be devised

that gives due credit to each of the variants in the two generations One method commonly used is the graphic method Thus each seed of the parent generation is measured and plotted on a graph in which the horizontal line (the abscissa) represents a series of size classes varying from the smallest ones at one end and the largest at the other and the perpendicular line (the ordinate) represents the frequencies of individuals in the varying size classes A line connecting high points in each of the size classes will form a *variation curve* which will be characteristic of the group Such a curve has a high point near the middle (called the *mode*) and the curve slopes gradually toward each end This curve not only represents the distribution of the different sizes in the group but shows the most commonly occurring size class the modal class A similar curve is made for the offspring generation and the parent curve is compared with the offspring curve The two may be compared with respect to mode mean, average, and standard deviation, and a great deal may be learned that can be learned in no other way about the variation and heredity of such graduated or fluctuating characters as weight

For further information about statistical methods in genetics the reader is referred to a short chapter in the Appendix (chap xliii) It will hardly be necessary here to do more than indicate that pure-line work such as that of Johannsen Jennings Tower and Wright discussed in the next chapter could not have been done without the use of biometrical methods

the mean annual rainfall and the general character and direction of air movements remain essentially the same for very long periods. Such constancy of environment could hardly fail to exercise a standardizing effect upon animal and plant communities and thus aid in maintaining constancy in the expression of racial characters.

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The first thing he did was to collect all the seeds (we would call them beans) from a single bean plant, which is a male female individual These beans were of many different sizes some quite large others quite small and many intermediate In order to follow the heredity of bean size with accuracy he weighed each bean on a delicate balance What he determined was the weight of each bean but we shall speak of large and small size instead of heavy and light weight Since some few of the beans were very large and some few very small what more natural than to select the largest beans to be the seeds for the next generation of plants, and to expect that the beans of the next and the next and the next generation would be larger and larger and larger?

If Johannsen was sanguine enough to expect to get such a rapid improvement in beans he was doomed to disappointment He had constructed a curve of variation in the manner described in the last chapter for beans of the parent plant This curve had a definite shape and a definite mode When he constructed a similar variation curve for the progeny derived from the largest beans of the first generation this curve was practically the same as that of the parent generation The beans were not all large as he may have hoped but some were large, some small and many intermediate just as in the parent generation Continuing to select, for planting the largest beans for six generations he found that there had been no change in the average size of beans, and the number of largest beans had not increased Selection then had been powerless when operating upon individuals with identical heredity

Another series of breeding experiments was carried out selecting for seed the smallest beans of the original parent plant of Pure Line I The bean progeny of the second generation differed not at all from those derived from the largest bean of this pure line They gave the same variation curve and the same average as the latter and this was maintained for six generations It made no difference whether the largest the smallest or the average beans were selected for planting so long as they belonged to the same pure line the same variation curve and the same average were maintained

A second pure line which we may call Pure Line II was started from another parent plant chosen because the average size of beans was distinctly less than that of the first pure line The statistical study of the beans of this second parent plant revealed another new and significant fact namely that the beans when arranged according to sizes gave a variation curve differing markedly from that of

Pure Line I The shape of the curve the mode and average size were different Again selection for six generations of first the largest beans for seed and second the smallest beans for seed did not affect the variation curve mode or average Once again selection within a pure line was quite ineffective

The same results were obtained in all the rest of the nineteen original pure lines with which Johannsen experimented

A somewhat more concrete idea of the results obtained may be secured through the perusal of the following table which gives in terms

RESULTS OF SELECTION IN PURE LINE I

Harvest Year	Mean Weight of Selected Parent Seed		Mean Weight Offspring	
	Minus	Plus	From Minus Parent	From Plus Parent
1902	60	70	63 15	64 85
1903	55	80	75 19	[illegible] 88
1904	50	87	54 59	56 68
1905	43	73	63 55	63 64
1906	46	84	74 38	73 00
1907	56	81	69 07	67 66

of average bean weight the results of selecting plus and minus parents for six generations in Pure Line I the plus parents being largest beans and minus parents being smallest beans

It will be seen that in the last year of this selection experiment (1907) the smallest beans averaging 56 cg in weight produced a progeny weighing on the average 69 07 cg while the largest beans of the same year averaging 81 cg produced progeny of practically the same average weight as did the smallest beans namely 67 66 cg The difference is not statistically significant The influence of the environment in bean weight is clearly shown in the data for the year 1904 which was a bad year for growth In this year the average weight of progeny from both large and small beans was greatly reduced being respectively 56 68 cg and 54 59 cg That this loss in weight was not inherited is shown by the results in subsequent years in which the average returned to that seen in the first year of selection It is also interesting to note that in the years 1903 1906 and 1907 the lighter parents produced a heavier progeny than did the heavier parents

From these experiments Johannsen came to the conclusion that plus and minus fluctuations about the mode were due to differences in

the environment and were not inherited, and that what was really inherited was merely a potentiality to produce beans of a certain average weight which may be modified by the environment It was also obvious that these environmental modifications had no effect on subsequent generations that is to say they are not inherited Selection therefore has no effect unless there are hereditary differences among the individuals selected

All the members of a given pure line are identical genetically that is there are no differences in their genes Johannsen called a group of individuals that are alike in their genes a *genotype* and spoke of all such individuals whether alike in seed size or not as *genotypically* identical Hence individuals that breed alike whether they look alike or not, are members of the same genotype On the other hand each of the nineteen pure lines is a different genotype though some beans in each pure line may be exactly of the same size as some beans in others Johannsen designated individuals that look alike and have the same somatic characteristics whether they are genotypically alike or not members of the same *phenotype* in other words they may be *phenotypically* identical though *genotypically* different Phenotypic differences unless also associated with genotypic differences are not hereditary This conclusion is a highly important one for all our further study of heredity

Another significant conclusion may be reached from these experiments namely that environmentally produced differences if they are merely phenotypic in character play no important part in evolution except in so far as they may favor the survival of certain individuals possessing genotypic differences Hence environmentally produced differences in the soma have only an indirect influence on the course of evolution

OTHER EXAMPLES OF PURE LINES

W L Tower in a long series of experiments on the potato beetle *Leptinotarsa decemlineata* came to similar conclusions He produced a pure line not by making use of a self fertilizing species but by closely inbreeding a bisexual family for a long time This stock was tested and found to be genotypically pure yet there was a considerable amount of variability in the shade of color in the color patterns and in other ways For twelve generations he selected and bred from the darkest specimens and from the lightest specimens keeping the two series separate (Fig 51) The result was that instead of getting

darker specimens predominating in one series and lighter specimens in the other he obtained a final generation of individuals showing practically the same range of variability in both series, and in neither series was there any consistent change from the condition present at the beginning of the experiment

More recently *Sewall Wright*, working in connection with the Bureau of Animal Industry, has produced a considerable number of pure lines by long continued brother and sister mating in guinea pigs Sixteen families have been established by over thirty generations of the closest possible inbreeding No selection was practiced The result was that most of the pure lines showed marked reduction in fertility and in vigor as compared with the control cross bred stock Each line, however, differed from all the others in these

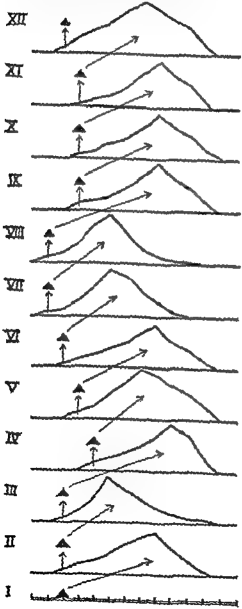


FIG 51 —Diagram to illustrate the results of selection in pure lines Ineffectiveness of selection through twelve generations within a homozygous strain in the case of the Colorado potato-beetle (*Leptinotarsa*) In each generation extreme dark specimens were selected as the parents of the succeeding generation but the progeny always swung back to the type (*After Tower*)

respects as well as in many others Members of any pure lines were remarkably uniform but there was also a fair amount of fluctuation with respect to quantitative characters Even such characters as the shape and extent of color markings weight fertility etc showed considerable individual variability but none of these differences proved to be hereditary

Jennings tried still another type of pure line material using organisms that reproduce by binary fission He worked with a number of differing clones (pure lines produced asexually) of Paramecium, a common ciliate protozoan Each selected Paramecium was isolated in a separate culture vessel where it was allowed to multiply for several generations Size differences and other measurable differences were noted in the original isolated parent individuals and those of all the progeny were measured plotted and averaged It was found that a different mean, mode and average size was characteristic for each pure line If the largest individual is then isolated from each culture and bred for a number of generations its progeny will be of the same average proportions as that of the stock from which the largest individual had been chosen for they are genotypically unchanged though differing phenotypically

Exactly what is inherited?—All that is passed on from one generation to another is an organized mass of protoplasm or in gametic reproduction two such organized masses—an egg and a sperm that unite to form a zygote Characters as such are not transmitted or passed on A zygote, the biologic heritage has no eyes no feet no brain no instincts All it possesses is a very definite nuclear and cytoplasmic organization which under an appropriate environment has the potentiality of producing a new individual with characters whose expression may be more or less modified by the differences in the environment within the organism or outside of it

Specifically let us state exactly what was inherited in Johannsen s pure lines Pure Line I differs in its hereditary potentialities from Pure Line II in that under the given conditions of the environment it produces on the average heavier beans than Pure Line II is able to produce If a particular bean chosen from Pure Line I and one from Pure Line II were allowed to develop under exactly the same environment the offspring of Pure Line I would be heavier than that of Pure Line II But if the environment of Pure Line II were better than that of Pure Line I it might readily produce larger beans that the latter But this environmentally induced difference would not be inherited

Exactly what then is inherited? A certain complex of genes and a certain cytoplasmic organization are all that can be said to be inherited. These heritages are to be conceived of as potentialities capable of working with the environment to produce individuals with certain particular characters. Individuals will differ from one another partly because the materials constituting the zygote are different and partly because their environments are different. To what extent heredity and environment determine individual differences we must not attempt to decide at present. We shall be in a much better position to deal with this problem after we have discussed the other factors of the evolution mechanism.

CHAPTER XVII

SEX DETERMINATION AND SEX DIFFERENTIATION

Introductory statement.—In chapter xiv we have spoken of sexual reproduction as one of the modes of cytogenic reproduction. We have also referred several times to the ways in which sexual reproduction constitutes the main mechanism of diversity. Two questions with regard to sex, however, have not yet been broached: (*a*) What determines the sex of the individual? (*b*) How do the secondary sexual characters of individuals develop? These two questions will be answered in the present chapter.

SEX DETERMINATION

The question as to what determines whether an animal shall be a male or a female is a very ancient one, and it is only during the present century that we have solved the puzzle.

A great many theories of sex determination have been proposed, some of which are as follows:

a) Hippocrates and some subsequent theorists believed that the sex of the offspring depended on the relative vigor of the parents, the more vigorous parent giving his or her sex to the offspring.

b) Thury thought that the sex of the offspring depended on the degree of ripeness of the ovum at the time of fertilization.

c) Various writers claim that statistics show that germ cells from the right ovary produce males and those from the left ovary females.

d) *The nutrition theory*.—The egg is a much more highly nourished cell than the spermatozoon, and the idea seems natural that high degrees of nourishment of the mother produce female offspring and lower degrees of nourishment male offspring. Professor Schenk of Vienna gained a huge reputation by controlling the diet of certain royal prospective mothers and predicting the sex of the offspring accordingly. He was correct in his predictions several times, but his success was short lived. His early predictions were merely lucky, just as one might be who could guess heads or tails correctly several times in succession.

Some color is lent to the nutrition hypothesis by the fact, if it is a fact, that after war or famine, when the nutrition of mothers has been

low, more males than females are born This is probably a case of differential prenatal mortality By that we mean that more females die unborn than males because the latter are hardier and stand pre natal malnutrition better

e) *Sex is determined at the time of fertilization* —Perhaps the best evidence that sex is determined at the very beginning of development

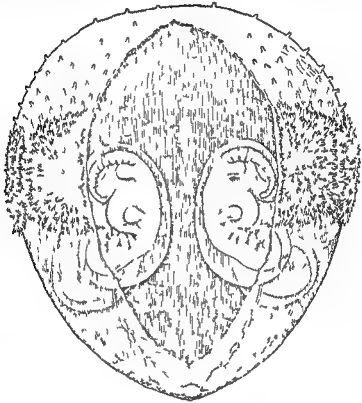


FIG 52 —An armadillo egg about six weeks after fertilization showing the quadruplet fetuses derived from the single egg and all destined to be of the same sex (*From Newman*)

is derived from one egg twins and quadruplets In the nine banded armadillo practically every female gives birth to quadruplets, four essentially identical young being produced in each litter All in a given set of quadruplets are invariably of the same sex either four males or four females Newman and Patterson have shown that each set of quadruplets comes from a single egg, which at a very early stage

divides into four parts to form four fetuses (Fig 52). The conclusion is that sex was determined before the separation took place Human identical twins also always of the same sex in a pair, furnish further evidence in favor of very early sex determination These and numerous other similar facts justify the conclusion that sex is determined at the time of fertilization

THE CHROMOSOMAL MECHANISM OF SEX DETERMINATION

In two previous chapters (chaps xv and xvi) descriptions of the typical modes of chromosomal sex determination have been given In order to facilitate a clear understanding of this important matter it seems well to recapitulate one typical instance Perhaps the best known instance of sex determination is that of *Drosophila melanogaster* already described and figured (Fig 53) by Babcock and Clausen In this insect the female body cells and the unmaturated germ cells are characterized by the presence of two sex chromosomes (X-chromosomes) which are shown in black at the top of the left hand column of the accompanying figure The chromosomes are readily distinguishable by being of medium size and straight The male body cells and unmaturated germ cells (top of right column) are just like those of the female except that there is substituted for one of the X-chromosomes a hook like chromosome, known as a Y chromosome Now in the process of maturation of the germ cells which results in the formation of gametes with the haploid or half somatic number of chromosomes, each of the eggs (female gametes) receives an X chromosome All eggs are therefore alike in their chromosome content, including the sex chromosome The case is different on the male side for two kinds of gametes are formed one kind with an X chromosome and the other with a Y chromosome These are formed in exactly equal numbers as one of each is produced at every reduction division Each egg must be fertilized by one or the other of these two kinds of sperms and in the long run as many eggs will receive an X-chromosome as will receive a Y chromosome Those that receive an X-chromosome will be characterized by having two X-chromosomes which is the typical female condition and thus a new female individual is started in life while those that receive no X chromosome but a Y-chromosome will have the XY composition characteristic of the male sex and will give rise to males The female sex may thus be designated as XX and the male sex as XY We have shown for *Drosophila* the exact mechanism that operates in determining whether an individual

shall be a male or a female and in addition we have explained why equal numbers of both sexes are continuously produced

How general is the chromosomal mechanism of sex-determina-

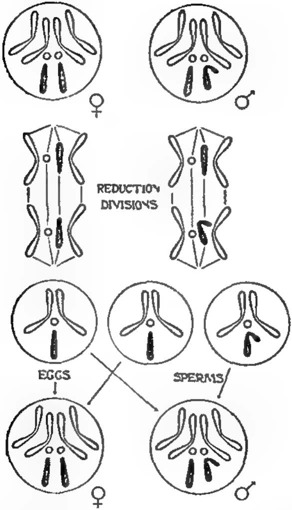


FIG 53 —Diagram showing chromosome relations in the determination of sex in *Drosophila ampelophila* (*From Babcock and Clausen*)

tion?— To what extent says E B Wilson sex may be determined by an automatically operating nuclear mechanism such as has been here described is unknown but a mechanism that exists in the same

general form in organisms as diverse as bryophytes nematodes echinoderms arthropods and vertebrates is beyond a doubt of far reaching significance, and may be as widely distributed as Mendelian heredity generally While the same general scheme holds for all forms that have been investigated there exist many interesting differences in the details of operation of the sex determining machine Some of the simpler variations of the process are as follows

a) *Variations of the Y-chromosome*—Beginning with a condition such as that described for *Drosophila* in which the Y chromosome is larger than the X chromosome there is a long series of species in which the Y chromosome becomes smaller and smaller until it dwindles away to nothing and the male chromosome condition becomes XO instead of XY In the females of such species the condition remains XX

b) *Variations of the X chromosome*—In a number of species of animals the X-chromosome may be represented by from two to nine components, each of which at times has the appearance of a separate chromosome In a species of roundworms *Ascaris canis*, for example the diploid chromosome number of the female is thirty six and that of the male is thirty the difference being due to the fact that there are two sets of six X components in the female and only one set in the male In the reduction division of the male germ cell the six X components all go in a group to one gamete and none to the other so that two kinds of gametes are produced one with eighteen chromosomes and the other with twelve chromosomes All the female gametes have eighteen chromosomes Apart from the fact that the X chromosome is in six pieces instead of but one the mechanism of sex determination is the same as it is in a group that has but one X chromosome

c) *Linkage of sex chromosome with autosome*—In a great many species of insects the X chromosome has been found to be united to one end of one of the autosomes never losing this relation during the entire chromosome cycle Apart from this apparently secondary union with an autosome, the behavior of the X chromosome is the same as in the XO cases described above Hence the mode of sex determination is in line with the types already discussed

d) *Female digamety*—In this mode of sex determination two different kinds of eggs are produced while the sperms are all alike In other words there is simply an exchange between the sexes of the nuclear differences characterizing males and females Thus in the Lepidoptera (butterflies and moths) the females have either the XY or the XO type of chromosome complex while the males always have the XX condi

tion Though the cytological evidence is still incomplete, it is practically certain that birds have the same peculiar method of chromosomal sex determination as the Lepidoptera, for they have the same type of sex linked heredity as the latter and the opposite of that seen in mammals and most insects Apart from the change of the digametic condition from one sex to the other the mechanism remains the same

Sex chromosomes in parthenogenesis—When it became known that parthenogenetic species (those in which eggs are capable of developing without fertilization) in some cases produce males and in other cases produce females from parthenogenetic eggs, this seemed to be out of accord with the theory of the chromosome mechanism of sex determination It is interesting to know however, that, now that we know the histories of the chromosome cycles in these species, the facts are not only fully in accord with the chromosome theory, but greatly strengthen it and enlarge its range of applicability Two kinds of parthenogenesis are known which may be designated *diploid* and *haploid* In the former, the developing egg and embryo has the full somatic number of chromosomes in the latter, only half the somatic number characteristic of the species is present

a) Diploid parthenogenesis—In these species only one maturation division occurs and this division is not the reduction division hence each egg retains the diploid number of chromosomes including two X-chromosomes (XX) The result is that all eggs that behave in this way develop into females Thus in aphids and phylloxerans many successive generations of all females are produced After a series of female generations, a mixed generation appears in which males are produced parthenogenetically along with females, but from smaller eggs Examination reveals the fact that male-producing eggs have after maturation two less chromosomes than the female-producing eggs This was explained by the observation that when the first maturation takes place two chromosomes (obviously consisting of a double X element) are cast out into the polar body, while all the autosomes and two of the X chromosomes remain in the egg nucleus In this way the male produced from this egg comes to have only two X-chromosomes while the female has four This is really the equivalent of XX for the female and XO for the male In gamete formation the males produce two kinds of gametes one with the double X-element and the other with no X element Only the former of these is viable, and this accounts for the fact that all fertilized eggs produce females for both gametes supply double X-elements Thus

whole rather intricate story is thus seen to be merely a variant upon the typical scheme of chromosomal sex determination

b) Haploid parthenogenesis —This kind of parthenogenesis is now known to occur in rotifers in several orders of insects and in arachnids It is practically universal among the Hymenoptera (bees wasps ants etc.) and we may use the case of the honey bee as an illustration In haploid parthenogenesis the egg develops after having undergone the reduction division it therefore has only half the somatic number of chromosomes including but one X chromosome Invariably the progeny from haploid parthenogenesis are males which we might expect from the fact that they have but one X-chromosome In the bees the queen seems to be able to determine whether an egg gets fertilized or not An egg descends the oviduct, passes the seminal receptacle containing a supply of sperms acquired during the mating act and if sperms are given off, fertilization occurs and a female is produced, but if an egg slips past the seminal receptacle without being fertilized the result is a male (drone) Now these drones are the mates of the future queens and must supply the spermatozoa for the next generation of eggs They already possess the reduced number of chromosomes so they cannot well undergo the reduction division in forming gametes It is interesting to note, however that a sort of vestigial reduction division takes place resulting in the formation of a tiny cell without any nucleus and a larger cell with all the chromosomes (including one X-chromosome) characteristic of males of the species A second maturation division divides chromosomes lengthwise Since all gametes both male and female contain an X chromosome fertilization always results in a female Thus once more the general sex determination formula is confirmed

Sex chromosomes in hermaphrodites and gynandromorphs —*Hermaphrodites* are individuals which are functionally both male and female that produce both eggs and sperms in the same body Hermaphroditism is common in snails flatworms earthworms nematodes tunicates, and in several other phyla of animals We have unfortunately very little information about the chromosome situations in these forms In one species of nematode (*Angiostomum nigrovenosum*) however it is known that there is an alternation of generations between a parasitic hermaphroditic generation and a free living dioecious generation (with separate males and females) In the dioecious generation males and females are about equally numerous All fertilized eggs of this generation produce parasitic hermaphrodites These produce from their gonads first oogonia and later spermatogonia the form

er producing eggs and the latter spermatozoa It is known that all eggs of the hermaphrodite generation have six chromosomes, while the sperms have either five or six Self fertilization takes place, and half of the fertilized eggs produce males with (eleven chromosomes) and half produce females (with twelve chromosomes) of the free living generation The males of the dioecious generation produce two kinds of gametes with respectively five and six chromosomes, and one would expect males and females to be produced from fertilization but this is not what happens, for only hermaphrodite individuals with twelve chromosomes are produced It eems certain that only one of the two kinds of spermatozoa (that with six chromosomes) is viable, and that the hermaphrodite generation is chromosomally female How can a female produce spermatozoa of two kinds, one with six and the other with five chromosomes? This is explained by the fact that in the second maturation division one of the X-chromosomes remains near the equator of the spindle, and does not become included within the daughter nucleus Thus one of the daughter cells is without an X chromosome and is male producing when fertilization takes place Further investigation of the chromosomes of hermaphrodites will doubtless be in agreement with what we already know

Gynandromorphs are individuals made up of some female body regions and some male body regions Thus, an insect may have male secondary sexual characters on one half of the body and female characters on the other or the anterior end may be male and the posterior female The chromosomal basis for these conditions is not entirely clear, but Morgan and Bridges have shown that all of the peculiarities of the hereditary behavior can be explained on the assumption that in the first or second cleavage division one of the X chromosomes lags behind and is excluded from one of the daughter cells Thus one daughter cell gets XX and the other X which accounts for the fact that all the cell descendants of one cell have the female characters and all those of the other cell male characters

Intersexes and their bearing on sex determination —Bridges, during his experiments with *Drosophila*, encountered in certain strains anomalous individuals that were neither male nor female but *intersexes* On cytological examination these were found to have a changed chromosome complex One type for example, was found to have three of one kind of autosomes (instead of the usual two) but only two X-chromosomes The interesexual condition in this case might be explained by the assumption that the autosomes have a male produc

ing tendency and that one set of extra autosomes is sufficient partially to overcome the female tendency of two X-chromosomes thus producing intersexes Again individuals with three X-chromosomes but only the usual supply of autosomes were super females somatically but unbalanced in their physiology and non viable These results show that in the words of E B Wilson *the actual performance of the zygote therefore is the common effect of the whole group and is turned this way or that as the result of a quantitative balance between X-chromosomes and autosomes*

SEX DIFFERENTIATION

It now becomes necessary to distinguish clearly between sex determination and sex differentiation When we say that by means of a chromosomal mechanism sex is determined exactly what do we mean? We answer that the sex of an individual arising from a fertilized egg (in the case of parthenogenesis an unfertilized egg) has been settled. Now as a matter of fact only one thing has been settled irrevocably and that is that one individual will have the chromosome composition characteristic of a male and another individual that of a female A male is usually an individual that produces spermatozoa and a female one that produces ova Is it irrevocably settled beyond possibility of reversal that a zygote with the XX chromosome composition must produce eggs and one with the X composition spermatozoa? This question has apparently been answered by Geoffrey Smith in his work on parasitically castrated crabs and by Richard Goldschmidt on Gypsy moths In the first case individual crabs whose testes had been infested by the parasitic cirripede *Sacculina* were gradually changed over in their whole metabolism to such an extent that cells destined to produce spermatozoa produced ova In the second case when certain varieties of moth were crossed all of the germ cells produced females with ova whereas half of the eggs had the XX and half the X chromosome content This evidently means that some individuals with the male chromosome character produced eggs From these results we may be justified in concluding that not even this most fundamental difference of sexes that of the female producing ova and the male spermatozoa is irrevocably predetermined at fertilization

Lest the reader be confused however we hasten to add that under natural conditions of life an individual with the male chromosomal content produces spermatozoa and one with the female chromosomal content produces eggs and that only rare accidental or unnatural

conditions disturb the normal course of events For purposes of practical genetics we may then define a female as an individual that produces ova and a male as one that produces spermatozoa

Secondary sexual characters—Usually males and females differ from each other in many other characters besides the production of eggs or sperm Often one sex is larger, stronger more elaborately ornamented and colored than the other and possesses characteristic accessory sex organs whose function it is to facilitate the bringing together of the eggs and the sperm All of the differences between the sexes other than the primary difference of egg or sperm production are called *secondary sexual characters* Usually very young animals show only slight differences in secondary sexual characters and the differences increase markedly at sexual maturity We speak of the gradual divergent development of the two sex types as sex differentiation The question arises as to whether or not the chromosomal differences are the causes of the differentiation of secondary sexual characters These secondary sexual characters are all somatic and since the soma is the product of cell division of the zygote the soma cells must have either the male or the female chromosomal character That the chromosomal mechanism in the somatic cells is not sufficient of itself to bring about unaided the differentiation of secondary sexual characters can be shown readily in at least many animals

In the mammals for example it is known that the early removal of the testes or ovaries results in a retention of the juvenile or undifferentiated condition of secondary sexual characters Evidently some influence is exerted by the tissues of the gonad that is necessary for the full differentiation of sex characters The current theory is that certain glandular cells that form part of the body of ovary or testes excrete materials into the blood that stimulate various tissues in different ways and produce dimorphic results The specific substances produced by these glands are called hormones for want of a better name To test the efficiency of these hormones the crucial experiment of taking out the gonads of a young rat or guinea pig and implanting the gonad of an individual of the opposite sex has been many times performed For example, Steinach castrated young male rats and then successfully grafted into them ovaries from young female rats The result was that these young rats which started to be males became much altered in a female direction, the mammary glands becoming greatly enlarged their instincts more feminine than masculine, and in a number of other particulars they showed more or less pronounced evidences of feminization Conversely spayed

females with engrafted testes showed a tendency toward male differentiation especially in instincts These experiments have been largely confirmed by C R Moore

In birds it is of interest to note that practically complete reversal of secondary sexual characters may be induced if young females are entirely deprived of the ovary The condition is described by L V Domm as follows

"The larger percentage of our birds have assumed additional male characters following removal of the ovaries until they are practically complete replicas of the male and, to those not familiar with their history they are regarded as unmistakable males Thus we find that they assume the complete male plumage, spurs grow as they do in the normal cock, head furnishings increase in size until they can not be distinguished from those of the normal male

Other birds in the pen regard them as males and when a strange cock is introduced they fight as would other cocks very frequently assuming the initiative some of them having been observed to come off victorious *in such a combat* *Many of these birds crow regularly* When aroused by a disturbance it was found that their reaction is very similar to that of the male the sounds they make, together with their reaction on such occasions reminds one very much of the young male just prior to maturity

'*One set of experiments may be mentioned as an example* Out of the one lot of fourteen females of the same hatch one was kept as control and thirteen were operated upon between the ages of six weeks and six months twelve of these have developed all the characteristics of the male mentioned above some being completely cock feathered while *the others are fast becoming so* *The other one of the thirteen* is very capon like in appearance except perhaps for size and can not be readily distinguished from her capon brothers by those not knowing her history This bird has assumed complete male plumage is developing spurs but the comb wattles and earlobes are pale and small *resembling those of the capon*

'In some of our cases individuals which have assumed more or less complete male characters as concerns head furnishings plumage and spurs are reverting toward the female type as shown by the female type of plumage reappearing

Our results indicate that the female in the brown leghorn fowl has many potentialities of the male which are normally inhibited by the presence of the ovary, and that these potentialities can assert

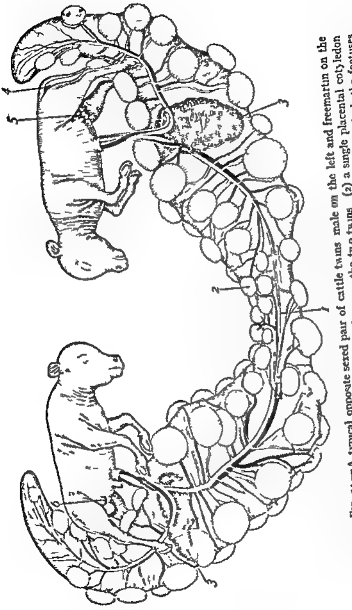


FIG 54 — A typical opposite sexed pair of cattle twins male on the left and freemartin on the right showing (1) the connecting artery between the two twins (2) a single placental cotyledon entered by veins from both foetuses (3) opening cut into the chorion through which the foetuses have been removed (4) clitoris of the freemartin (5) the well separated anterior and posterior teats characteristic of the female (6) the much closer teats characteristic of the male (*From Newman after Lillie*)

themselves approximately fully after the complete removal of the ovary at an early age'

A beautiful experiment conducted by nature herself helps to drive home the *hormone theory of sex differentiation* In cattle as shown recently by F R Lillie, twins occur in a small percentage of cases and involve the simultaneous fertilization of two eggs These eggs lie as a rule in opposite horns of the forked uterus but owing to the growth of their embryonic membranes the two individuals come to fuse circulations so that there is an admixture of blood (Fig 54) The result is that if the twins are zygotically of the same sex no untoward effect of blood admixture is apparent but when the twins are zygotically a male and a female the female individual is always stopped in its female differentiation and becomes more or less completely transformed in a male direction It appears however, that at the time when blood admixture occurs the female individual has already differentiated so far with respect to the external genitalia and in other respects that, even though subsequent development be entirely male in character, the resultant individual is always a sterile creature neither fully a female nor a complete male Such individuals have long been known as freemartins As a rare exception to the general rule an occasional case has appeared in which a male and a female pair fail to undergo blood admixture In such cases both develop into normal animals It now appears that the reason why the female sex is the one to suffer is that the male gonads differentiate precociously before the female and inhibit the subsequent development of female gonads Hence the only hormones in the blood of both twins are the male hormones

In conclusion we may say then that in mammals though chromosomes tend to determine the primary sex differences they have no effect on the differentiation of secondary sexual characters These are due to substances secreted by the gonads that have been called hormones

CHAPTER XVIII

MENDEL'S LAWS OF HEREDITY

MENDEL'S LIFE AND CHARACTER

J. ARTHUR THOMSON

Gregor Johann Mendel was born in 1822, the son of well-to-do peasants in Austrian Silesia. He became a priest in 1847, and studied physics and natural science at Vienna from 1851 to 1853. Thence he returned to his cloister and became a teacher in the Realschule at Brunn. It was his hobby to make hybridisation experiments with peas and other plants in the garden of the monastery, of which he eventually became abbot. Apart from two papers, one dealing with peas and a shorter one with hawkweeds, and some meteorological observations, he does not seem to have published much. But what he did publish, if small in quantity, was large in quality. He died in 1884.

MENDEL'S DISCOVERIES

In 1866 Gregor Johann Mendel, Abbot of Brünn, published what some regard as one of the greatest of biological discoveries. After many years of patient experimenting, chiefly with the edible pea, he reached a very important conclusion in regard to the inbreeding of hybrids, which is often briefly referred to as "Mendel's Law." His publication was practically buried in the Proceedings of the Natural History Society of Brunn; those who knew of it, as Nageli for instance did, failed to realise its importance; in fact, Mendel's epoch-making work was lost sight of amid the enthusiasm and controversy which the promulgation of Darwinism (1858) had evoked. Mendel's Law seems to have been rediscovered independently in 1900 by the botanists De Vries, Correns and Tschermak, and to Mr. Bateson we owe much not only for his recognition of the far-reaching importance of the abbot's work, but also for a notable series of experiments in which he has confirmed and extended it.

From J. Arthur Thomson, *Heredity* (copyright 1907). Used by special permission of the publishers, John Murray, London.

Mendel s experiments —What Mendel sought to discover was the law of inheritance in hybrid varieties and he selected for experiment the edible pea (*Pisum sativum*) The trial plants, he says, must possess constant differentiating characters and must admit of easy artificial pollination, the hybrids of the plants must be readily fertile and readily protectable from the influence of foreign pollen These conditions were afforded by peas, and twenty two varieties or subspecies of pea were selected which remained constant during the eight years of the experiments Whether they were called species, or sub species or varieties is a matter of convenience the names *Pisum quadratum P saccharatum, P umbellatum*, etc do in any case represent groups of similar individuals which breed true *inter se* It should be noted that these peas have the particular advantage, for experimental purposes that they are habitually self fertilised—in North Europe, at least

In studying the different forms of peas Mendel found that there were seven differentiating characters which could be relied on

1 The form of the ripe seeds whether roundish with shallow wrinkles or none, or angular and deeply wrinkled

2 The colour of the reserve material in the cotyledons—pale yellow bright yellow, orange, or green,

3 The colour of the seed coats, whether white as in most peas with white flowers or grey, grey brown leather brown with or without violet spots, and so on,

4 The form of the ripe pods whether simply inflated or constricted or wrinkled

5 The colour of the unripe pods whether light or dark green or vividly yellow, this colour being correlated with that of stalk, leaf veins and blossoms,

6 The position of the flowers whether axial or terminal and

7 The length of the stem whether tall or dwarfish

Mendel s results the Law of Dominance —Having defined the differentiating characteristics of the varieties Mendel proceeded to make crosses between these, investigating one character at a time Thus pollen from a pea of the round seeded variety was transferred to the stigma of a pea of the angular seeded variety the stamens of the artificially pollinated flower being of course removed before they were ripe The same was done all along the line

What was the result in the hybrid or cross-bred offspring? It was found that they showed one of each pair of contrasted characters to

the total or almost total, exclusion of the other No intermediate forms appeared

Mendel called the character that prevailed dominant, and the character that was suppressed or apparently suppressed recessive And the first big result was that crosses between a plant with the dominant character and a plant with the recessive character yielded offspring all resembling the dominant parent as regards the character in question Let us for shortness call the parents D and R, and the first result may be expressed thus $D \times R = D$

It must be carefully noted that the *complete* dominance which Mendel observed has been shown in other cases to be the exception rather than the rule Thus a cross between a 'Chinese' primula with wavy crenated petals and a "star" primula with flat simply notched petals is intermediate between the two parents, and yet as the next generation shows, the case is one of Mendelian inheritance

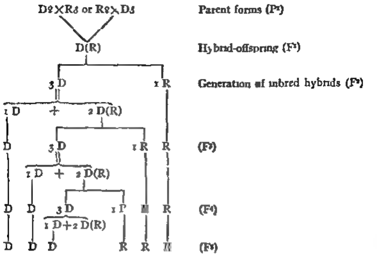
In many cases the hybrid while on the whole dominant may show some influence of the recessive character but not nearly enough to warrant us in speaking of a blend Thus, when white (dominant) Leghorn poultry are crossed with brown (recessive) Leghorn, most of the offspring have some 'ticks' of colour When these are inbred they produce a quarter brown (extracted recessives) and three-quarters pure white or white with a few ticks The dominance is not quite perfect

The Law of Splitting or Segregation.—In the next generation the cross-bred plants (products of D and R or R and D but all apparently like D) were allowed to fertilise themselves, with the result that their offspring exhibited *the two original forms*, on the average three dominants to one recessive Out of 1 064 plants 787 were tall, 277 were dwarfs

When these recessive dwarfs were allowed to fertilise themselves they gave rise to recessives only for any number of generations The recessive character bred true

When the dominants on the other hand were allowed to fertilise themselves, one third of them produced 'pure dominants which in subsequent generations gave rise to dominants only and two-thirds of them produced once again the characteristic mixture of dominants and recessives in the proportion of 3 1

The general results may be expressed in the scheme The result of the hybridisation is a generation (F) like the dominant parent They may be represented by the symbol D(R) for they



carry with them the possibility of having offspring with the recessive character that is to say the recessive character remains latent in the inheritance

When these D(R)s are inbred (self fertilised in the case of peas) they have offspring (F), some of which resemble the recessive parent while other resemble the dominant parent and these occur in the proportion of 1 3 When those resembling the recessive parent are inbred they breed true—i e they give rise to a line of pure recessives Those resembling the dominant parent are all apparently alike but their subsequent history shows that they may be divided into a set which breed true to the dominant type and a set which behave like the first generation of hybrids—i e they go on splitting up into dominant like forms and pure recessives These two sets occur in the proportions of 1 2

A case of peas —Let us consider a concrete case Peas with rounded seeds were crossed with peas having angular wrinkled seeds In the offspring the character of roundness was dominant the angular wrinkled character had disappeared or receded It was not *lost* as the next generation showed

The hybrid offspring all with rounded seeds, were allowed to self fertilise In their progeny roundish seeds and angular wrinkled seeds occurred in the proportions of 3 1 Here were the recessives again and when *they* were allowed to self fertilise they produced pure recessives only with angular wrinkled seeds

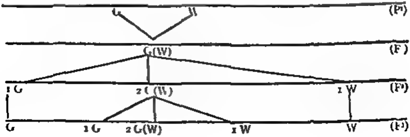
The dominants however were not all pure dominants, for when they were allowed to self fertilise they produced one-third pure dominants and two thirds 'impure' dominants, the latter being distinguished by the fact that in their offspring recessives reappeared in the proportion of one recessive to three dominants.

The outstanding facts, taking the case of yellow seeded and green seeded peas, may be thus summarised:—

Parental Generation (P1)	Yellow seeded pure plant (dominant)		Green seeded pure plant (recessive)
First Filial (hybrid) Generation (F1)	All the offspring were yellow seeded. Self fertilised they yielded		
Second Filial (inbred) Generation (F2)	Yellows (pure type)	Yellows (impure type)	Greens (pure type)
Third Filial (inbred) Generation (F3)	Yellows (pure type)	Yellows (pure) · Yellows (impure) · Greens (pure)	Greens (pure type)

Thus intercrossing of forms with contrasted characters results not in transitional blends but in the dominance of one character and the recession of another. Self fertilisation (the extreme of inbreeding) of the hybrids results in a number of pure recessives and a number of dominants in the proportion 1 : 3; some of these dominants (one-third) are pure, and produce only dominants; some (two-thirds) are apparently pure but produce dominants and recessives in the old proportion, 3 : 1.

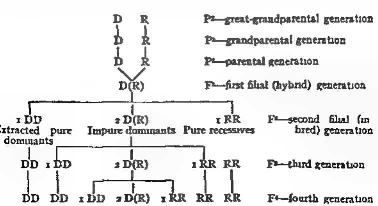
A case of mice.—Let us take a concrete case from among animals. A grey house mouse is crossed with a white mouse; the offspring are all grey. Greyness is dominant, albinism is recessive.



The grey hybrids are inbred, their offspring are grey and white in the proportion 3 : 1. If these whites are inbred they show themselves "pure," for they produce whites only for subsequent generations. But when the greys are inbred they show themselves of two kinds, for one-third of them produce only greys which go on producing greys, while the other two-thirds apparently the same produce both greys and whites. And so it goes on.

Summary.—In his exceedingly clear exposition of Mendelism (1905) Mr. R. C. Punnett states the result thus: "Wherever there occurs a pair of differentiating characters of which one is dominant to the other, three possibilities exist: there are recessives which always breed true to the recessive character; there are dominants which breed true to the dominant character, and are therefore pure; and thirdly, there are dominants which may be called impure, and which on self fertilisation (or in breeding where the sexes are separate) give both dominant and recessive forms in the fixed proportion of three of the former to one of the latter."

Schematic representation of Mendel's Law.—Following Mr. Punnett's suggestion, with slight modifications, we may use the symbols P_3, P_2, P_1 for the parental, grandparental and great grandparental generations; F_1 for the first filial (hybrid) generations; F_2, F_3, F_4 for the subsequent inbred generations. The symbol D(R) means a dominant with the recessive character unexpressed but potentially present; DD or RR means pure "extracted" dominants or recessives—i.e. those pure forms which are sifted out from the inbreeding of "impure" dominants.



MENDEL S EXPLANATIONS

JOHN M COULTER AND MERLE C COULTER

Mendel s explanation of this behavior involved three theses which at that time were new to biology [1] These theses must be kept distinct from one another

1 Independent unit characters —This means that an organism although representing a morphological and physiological unity, from the standpoint of heredity is a complex of a large number of independent heritable units Thus if one pea plant is tall and another one is dwarf the behavior of the hybrid produced from them with reference to this character will be the same no matter what other characters the parent plants may have had In other words, the characters are *independent units* unaffected by other characters or units The character of tallness from a tall plant with wrinkled seeds or purple flowers will act just the same as from a tall plant with smooth seeds or white flowers Tallness is a unit and its behavior in inheritance is independent of all other units

2 Dominance —In the germ plasm there are certain determiners of unit character which dominate during the development of the body causing these characters to dominate over others and thus become visible The characters dominated over and thus not allowed to express themselves are called *recessive* characters These recessive characters are present in the germ plasm, but cannot express themselves and become visible as long as the *dominant* characters are present. When a dominant character is absent however its recessive alternate is free to express itself and become visible

For example in the case of tall and dwarf peas, tallness is a dominant character and dwarfness is its alternative recessive When a dwarf appears therefore, there is present no dominant tallness to suppress it In the F_1 generation all the individuals were tall because although they had all received the recessive character of dwarfness from one of the parents they had received the dominant character of tallness from the other parent and so dwarfness did not appear in any of them Such pairs of alternative characters are now commonly called *allelomorphs* Thus tallness and dwarfness are allelomorphs in the pea one dominant over the other which is therefore recessive

3 Purity of gametes —A gamete can contain only one of two alternative characters For example, it may contain the character

[1] From Coulter and Coulter *Plant Genetics* (The University of Chicago Press copyright 1918)

for tallness or for dwarfness, but not both In other words allelo morphs cannot be represented in the same gamete If the gamete having the character for tallness unites with one having the character for dwarfness the resulting zygote will contain both, but will produce a tall individual because tallness is dominant over dwarfness When this tall hybrid produces gametes however one half of them will contain the character for dwarfness . Thus the alternative characters are segregated ' in gamete formation and no gamete will have both characters

These three theses, independent unit characters, dominance, and purity of gametes (better called segregation) make up the theoretical explanation of Mendel s law Independent unit characters was of course a necessary conception . It was original with Mendel, and has also been original with other investigators, but this conception does not represent the essential feature of Mendel s law The idea of domi nance had been somewhat vaguely proposed before Mendel s time In the old literature on animal breeding one meets theories of pre potency which were proposed again and again before the discovery of Mendel s work in 1900 In any event Mendel was the first to formulate definitely the theory of dominance among unit characters It should be realized also that dominance is not an essential feature of Mendel s theory Many cases are known in which dominance fails but in other regards the Mendelian inheritance is strictly followed

The essential feature of Mendel s theory is his conception of the *purity of gametes* brought about by the segregation of alternative characters The striking fact is that this conception, purely theoreti cal with Mendel has since been confirmed by cytology In the mechanism of cell division each chromosome is divided into two equal parts and each daughter cell receives one of these parts It is a reasonable inference that chromosomes are bearers of hereditary characters In the production of gametes the number of chromosomes characteristic of the organism is reduced one half As a consequence each gamete carries only one half the characters of the individual that produced it An application of these statements to an explanation of Mendel s 3 1 ratio will illustrate the situation

For convenience we will assume that the nuclei of Mendel s peas have four chromosomes each (Fig 55) In the case of a tall plant two of the four chromosomes carry the character for tallness that is some thing that determines the production of the tall character in the somatoplasm which is practically the *body builder* This unknown

something is called by various names in the literature of genetics the commonest one being *determiner* In our illustration, therefore two of the four chromosomes carry the determiner for tallness At this point two questions may be asked

1 Why do just two of the four chromosomes carry the determiner for tallness rather than all of them or only one of them? Just here it would be difficult to explain why no more than two of the four chromosomes are represented as carrying the same determiner This will be explained later It is easy to answer, however, why the determiner is being carried by more than one chromosome When gametes are formed the chromosome number is reduced one half Since every gamete from a pure tall plant carries the determiner for tallness there

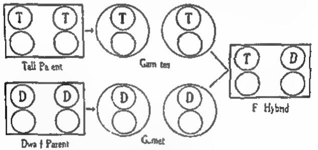


Fig 55 —Diagram illustrating behavior of chromosomes in Mendel's cross of tall and dwarf peas Large rectangular figures nuclei of zygotes or mature individuals large circles gametes small circles within zygotes and gametes chromosomes letters on chromosomes determiners (T tallness D dwarfness) (*From Coulter and Coulter*)

must have been at least two chromosomes carrying the determiner before the gametes were formed

2 Do these two chromosomes carry any other determiner than that for tallness? In a tentative way this question may be answered in the affirmative but a fuller discussion of the situation must be deferred There is much experimental evidence that indicates that more than one determiner is carried on a single chromosome In some cases also there are more Mendelian determiners than there are chromosomes

The situation is represented in Figure 55 This shows a somatic cell with the diploid or $2x$ number of chromosomes In the formation of gametes this number is reduced to the haploid or x number which in this case is two The diagram shows that the reduction separates

(segregates) the two chromosomes carrying the character for tallness so that each gamete contains one. This occurs for the other characters as well as for that of tallness. From the tall plant, therefore, all the gametes will contain the character for tallness, and from a dwarf plant all of the gametes would contain the character for dwarfness. When these two individuals are crossed the zygote will contain both characters and these two characters will be transmitted together in the succeeding cell generations. The individual from such a zygote of course would be tall but at the same time it would be carrying a recessive determiner for dwarfness and this fact would be shown by

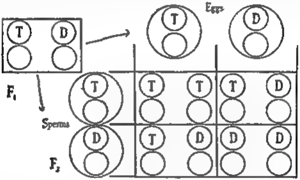


FIG 56.—Diagram illustrating behavior of first hybrid generation (F_1) when inbred. Illustrates meaning of segregation and purity of gametes and how chance matings of F_1 gametes result in 3 : 1 ratio in F_2 generation; dwarf individual produced only by zygote in lower right hand corner. (*From Coulter and Coulter.*)

its behavior in breeding. The result of inbreeding such hybrids is indicated in the accompanying diagram (Fig. 56) which represents the chance matings of two kinds of gametes. The obvious results are three tall individuals and one dwarf. This is the so-called *monohybrid ratio* which means the ratio when a single pair of allelomorphs is considered.

Before discussing the further development of Mendel's law it will be necessary to explain some of the terminology of genetics. When each gamete carries the same kind of determiner the zygote is said to receive a *double dose*; when a zygote receives only a single such determiner it is said to receive a *single dose*. In Figure 56 one zygote receives a double dose of tallness and two others a single dose. These phrases are more or less common in the literature of the subject but the more

frequent terminology is as follows When two similar gametes unite to form a zygote it is called a *homozygote* when the two pairing gametes are different the zygote is called a *heterozygote* Using this terminology it is evident that the 3 1 ratio of the F generation is really a 1 2 1 ratio as follows 1 homozygote for the dominant character 2 heterozygotes and 1 homozygote for the recessive character The 1 2 1 ratio therefore is the significant one and appears as a 3 1 ratio only because of dominance

In the experiment represented in Figure 56 three tall individuals appear in the F generation Superficially the individuals look alike but it is realized that 1 differs from the other 2 in germinal constitution for 1 will produce only one kind of gamete while the other 2 will produce two kinds To indicate this situation Johannsen has introduced some appropriate terminology Organisms which seem to be alike regardless of their germinal constitution are said to be *phenotypically* alike or to belong to the same *phenotype* On the other hand organisms having identical germinal constitution are said to be *genotypically* alike or to belong to the same *genotype* From the standpoint of phenotypes only Mendel s F generation shows the 3 1 ratio but if genotypes are considered it shows the 1 2 1 ratio In other words this group of forms contains two phenotypes but three genotypes

Referring again to Figure 56 several things may be inferred It can be seen what will happen in the F_3 generation when the F individuals are inbred The dominant homozygote will produce only dominant homozygotes in the F_3 generation and will continue to produce them as long as it is inbred The two heterozygotes will split up in the F_3 generation in the same 1 2 1 ratio as did their hybrid parents of the F_2 generation The recessive homozygote will produce only recessive homozygotes as long as it is kept pure by being inbred

It is interesting to consider what will happen if a heterozygote form is crossed with a homozygous recessive It should be obvious that one half of the progeny would be pure recessives, while the other half would be heterozygotes that is there would be a 1 1 ratio A similar result would be obtained by crossing a heterozygote with a dominant homozygote although all the immediate progeny would show the dominant character The real situation would be revealed, however, when this progeny was inbred, for one half would be homozygous (pure breeders) and the other half would be heterozygous (hybrid breeders)

Thus far we have considered only what is called the monohybrid ratio that is the ratio obtained from one pair of contrasting characters such as tallness and dwarfness The next step is to consider the dihybrid ratio Mendel also used contrasting seed characters finding for example that smoothness in seeds is dominant to a wrinkled condition Introducing this pair of contrasting characters into the situation we have been considering the dihybrid ratio will be the result Crossing a tall smooth seeded individual with a dwarf wrinkled seeded individual it is evident that all of the F or first hybrid generation will be tall smooth seeded individuals since both of these characters are dominant In the F generation however the following ratio will appear 9 tall smooth 3 dwarf smooth 3 tall wrinkled 1 dwarf wrinkled which is a 9 3 3 1 ratio This is the dihybrid ratio the explanation of which may be indicated in Figure 57 The question may be raised why the characters for tallness and smoothness are not represented on the same chromosome If they were the result would be a simple monohybrid ratio except that the tall individuals would always be smooth seeded as well and dwarfs would be always wrinkled seeded The possibility of one chromosome carrying two different determiners will be considered later but at present we shall assume that these determiners are on different chromosomes

Figure 57 shows that we are dealing with two homozygotes each producing only one kind of gamete so that all the hybrid progeny will be similar both genotypically and phenotypically that is with the same germinal constitution and the same appearance By inbreeding these F individuals it will be seen that four kinds of gametes are involved Crossing these four kinds of gametes the resulting combinations are indicated in Figure 57 The result is four phenotypes as follows Nos 1 2 3 4 5 7 9 10 13 are tall smooth individuals Nos 11 12 15 are dwarf Nos 6 8 14 are tall wrinkled No 16 is dwarf wrinkled This is the 9 3 3 1 ratio

It will be noticed that Nos 1 6 11 16 are homozygotes and therefore will breed true but the rest are heterozygotes either for one pair of characters or for both and these would split into various types upon further breeding

The next step is the trihybrid ratio Mendel found yellow seeds dominant over green seeds and if this pair of characters is included with those used above the trihybrid result can be observed The experiment would consist in crossing tall smooth yellow individuals with dwarf wrinkled green individuals and it is obvious that the

hybrid progeny would all be tall, smooth, yellow, since these three characters are dominant Inbreeding the hybrids gives the following result in the F_2 generation 27 tall smooth yellow, 9 tall smooth green,

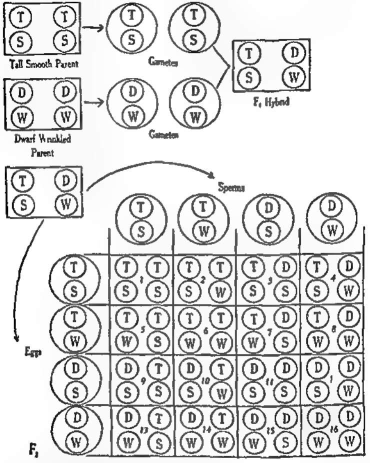


FIG 57 —Diagram illustrating dihybrid ratio Upper part shows how original parents were crossed to give F_1 hybrid lower part shows F_1 hybrid producing four kinds of gametes chance matings among these gametes when F_1 is inbred result as indicated in the large set of squares and explains the 9 3 3 1 ratio in the F_2 generation (*From Coulter and Coulter*)

9 tall wrinkled yellow, 9 dwarf smooth yellow 3 tall wrinkled green, 3 dwarf smooth green, 3 dwarf wrinkled yellow 1 dwarf wrinkled green The trihybrid ratio therefore is 27 9 9 9 3 3 3 1 This involves 64 individuals and 8 phenotypes

ILLUSTRATIONS OF SIMPLE MENDELIAN INHERITANCE IN BOTH ANIMALS AND PLANTS[1]

J ARTHUR THOMSON

How far has Mendel's experience been confirmed?—There has been confirmatory work by Correns (on peas, maize and garden stock) by Tschermak (on peas) by De Vries (on maize etc), by Bateson and his collaborators (on a large variety of organisms) by Darbishire (on mice), by Hurst (on rabbits) by Toyama (on silk moths) by Davenport (on poultry) and so on There are some difficulties and not a few discrepancies but as Bateson says ' the truth of the law enunciated by Mendel is now established for a large number of cases of most dissimilar characters "

In experimenting with *Lychnis*, *Atropa* and *Datura* Bateson and Saunders found that the phenomena conformed with Mendel s law ' with considerable accuracy and no exceptions that do not appear to be merely fortuitous were discovered. In the case of *Matthiola* (garden stock) the phenomena are much more complex There are simple cases which follow Mendelian principles but others of various kinds which apparently do not The latter cases fall into fairly definite groups but their nature is obscure

In experiments with poultry, the phenomena of dominance and recession were detected interbreeding of the hybrid offspring resulted in a mixed progeny some presenting the dominant others the recessive character in proportions following Mendel s Law with fair consistency though in certain cases disturbing factors are to be suspected

The general result, so far is that Mendel s law has received confirmation in a number of very dissimilar cases

Dominant and recessive characters—Let us first of all collect a number of instances of contrasted characters which behave in relation to one another as dominants and recessives

	Dominant	Recessive
Pisum sativum	Tallness	Dwarfness
	Round seeds	Wrinkled seeds
	Coloured seed-coats	White seed-coats
	Yellow albumen in cotyledons	Green albumen in cotyledons
	Purple flowers	White flowers
Sweet pea	Tall ordinary form	Dwarf or cupid variety

[1] From J Arthur Thomson, *Heredity* (copyright 1907) Used by special permission of the publisher John Murray London.

	Dominant	Recessive
Stocks	Coloured	White
Wheat and barley	Beardless	Bearded
	Later ripening Rivett wheat	Early ripening Polish wheat
	Non immune to rust	Immune to rust
Maize	Starch seed	Sugar seed
Nettles (*Urtica pilulifera* and *U dodartii*)	Serrate leaf margin	Entire leaf margin
Mirabilis jalapa and *M rosea*	Rose colour	Other colours
Mice	Coloured coat	Albino coat
	Normal	Waltzing variety
Rabbits	Coloured coat	Albino coat
	Angora fur	Short fur
Poultry	Rose comb of Hamburghs and Wyandottes	High serrated single comb of Leghorns and Andalusians
Cattle	Hornlessness	Horns
Snails	Bandless shell	Banded shell

Other instances in plants —As is well known, there are two almost equally common forms of wild primrose (A) thrum types with short styles and with anthers at the top of the corolla tube, and (B) pin types with long styles and with anthers half way down the tube The thrum type is dominant over the pin type

The original species of Chinese primrose (*Primula sinensis*) has a palmate leaf About 1860 a sport arose (from seed) which had a pinnate or fern leaf The palmate form is dominant and the fern leaf is recessive

The deformed "Snapdragon" variety of sweet pea behaves as a recessive to the normal type

The 2 row barley has certain lateral flowers which are exclusively staminate in 6 row barley all the flowers are staminate and pistillate and all set seed Mr Biffen crossed these forms and found that the more negative character was dominant The offspring were 2 rowed

Maize —When the common or starchy round seeded maize is crossed with the wrinkled seeded sugar maize the round starchy character dominates When an egg-cell of the wrinkled sugar maize stock is fertilised by a pollen cell of the round starchy stock the result is a round seed with starchy endosperm If this seed is sown, it becomes a plant which on self fertilisation forms a cob with a mixture of round starchy and wrinkled sugary seeds in the ratio 3 1 The wrinkled seeds yield sugar maize the round seeds yield two "impure rounds" to one "pure round" Correns has observed a very interesting case in which two pairs of contrasted characters are implicated

One variety *Zea mays alba* which has *smooth* white seeds was crossed with another variety, *Zea mays coeruleodulcis* which has wrinkled *blue* seeds The hybrids (F_1) had *smooth blue* seeds one character of each parent being dominant, and one character of each parent being recessive The hybrids were inbred, and the progeny (F) showed four combinations—*smooth blue*, *smooth* white, wrinkled *blue*, and wrinkled white (the dominant characters are italicised)

In the next generation (F_3) the wrinkled white, inbred yielded wrinkled white—a case of extracted recessives breeding true The *smooth* whites and wrinkled *blues*, inbred, yielded partly forms like themselves and partly wrinkled white The *smooth blues* inbred, yielded the same combinations as in F_2

A finer corroboration of Mendelian could hardly be wished.

Nettles —Correns crossed two ' species of stinging nettle " *Urtica pilulifera L* and *U dodartu L*, which resemble one another except as regards leaf margin strongly dentate in the former almost entire in the latter The hybrid offspring (F_1) have all dentate leaves like the male or the female parent as the case may be The dentate character is absolutely dominant The inbred (self fertilised) hybrids produce offspring (F) of two kinds with dentate and with entire margins on an average in the Mendelian proportion, 3 1

' Immunity to rust in wheat.—Some kinds of wheat are very susceptible to the fungoid disease known as rust' others are immune The quality of immunity to rust is recessive to the quality of predisposition to rust

When an immune and a non immune strain are crossed together the resulting hybrids are all susceptible to 'rust On self fertilisation such hybrids produce seed from which appear dominant rusts and recessive immune plants in the expected ratio of 3 1 From this simple experiment the phrase resistance to disease' has acquired a more precise significance and the wide field of research here opened up in this connection promises results of the utmost practical as well as theoretical importance To the question Who can bring a clean thing out of an unclean? we are beginning to find an answer nor is the answer the same as that once given by Job (R C Punnett)

Silkworms —Toyama paired Siamese silkmoths with yellow or with white cocoons the offspring produced only yellow cocoons When the hybrids were inbred the result was two sets one producing white cocoons, the other producing yellow cocoons and the proportion was Mendelian—25 037 white and 74.96 yellow The whites bred

true, the yellows when inbred showed themselves to be pure dominants or yellows" and dominant recessives—i e, splitting up again into yellows and whites in the usual proportion More intricate experiments confirmed this general result

It must be noted however, that Coutagne has made much more elaborate experiments with different results which in *many* cases can not be interpreted on the Mendelian theory Thus he found (1) that the hybrid forms were sometimes blends of the parents and different from both (2) that in other cases the brood included some like one parent in a particular character, some like the other parent, and some intermediate and (3) that in other cases the individuals showed no fusion of characters but resembled one or other parent It is likely that the discrepancy may be explained as due to considerable diversity of origin in the domesticated races of silkworm so that, while they breed true when left to themselves, a disturbance of the usual routine leads to the liberation of latent characters

Lina lapponica —Miss McCracken has made a fine study of the hereditary relations in this Californian beetle which occurs in two types, spotted (dominant) and black (recessive) They are always crossing in natural conditions, but there are no intermediates, and it is easy by isolation to rear a ' pure spotted race and a "pure" black race When spotted forms are paired they may produce only spotted progeny—a case of extracted dominants In other cases however they yield spotted and black forms (1 021 spotted 345 black), i e, in the Mendelian proportion of 3 1—a case of dominant recessives inbred

Snails —Lang paired pure five banded forms of the common or garden snail *Helix hortensis*, with bandless forms from bandless colonies The young of the first generation were all bandless the banded character being recessive When these were paired the off spring were bandless and banded in the Mendelian ratio, 3 1 Further experiments confirmed this not only as regards bands, but also as regards colour (yellow or red), size and the form of the umbilicus *It may be said, therefore that common snails (Helix hortensis and Helix nemoralis) illustrate Mendelian inheritance*

Poultry —Numerous breeding experiments with poultry have been made by Bateson Bateson and Punnett Hurst Davenport and others many of which show Mendelian phenomena with great clearness while others are strangely conflicting One of the reasons for the complicated results is evidently to be found in the difficulty of securing thoroughly pure ' breeds for many that breed true as long as they

are inbred tend to liberate latent characters when the ordinary course of breeding is departed from.

Hurst contrasts the following characters which usually show them selves dominants and recessives but it has to be admitted that the dominance—always complete for some characters—is for others fre quently, or even always incomplete—i.e showing traces of the corresponding recessives

Dominant Characters	Recessive Characters
Rose comb	Leaf comb single comb
White plumage	Black plumage, buff plumage
Extra toes	Normal toes
Feathered shanks	Bare shanks
Crested head	Uncrested head
Brown eggs	White eggs
Broodiness	Non broodiness

Davenport s copiously illustrated work is also of great interest He shows in case after case that the character dominant in the first hybrids is more or less influenced by the recessive character Polish fowls with a large hernia of the brain on the top of the head were paired with Minorcas with normal heads The hybrids showed no hernia but most of them showed a frontal prominence When the hybrids were inbred the hernia occurred in 23 5 per cent—a close approximation to the theoretical 25 per cent.

Single combed black Minorcas were crossed with white crested black Polish fowls with a very small bifid comb The hybrids had combs single in front split behind When the hybrids were inbred there resulted in a total of 101 offspring 29 7 per cent with single combs (like Minorcas) 46 5 per cent with Y-shaped combs and 23 8 per cent with no combs or only papillae (like the Polish forms) Here again the result is in a general way Mendelian but the Y like comb is a complication

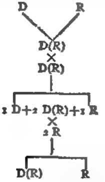
Pigeons —R Staples-Browne crossed a web footed pigeon (an occasional discontinuous variation) with a normal form and got six normal young In other words the web foot character is recessive to the normal foot character The hybrids were inbred and in one case produced nine with normal feet and three with webbed feet—a Mendelian splitting up But from another pair of hybrids seventeen *normal offspring resulted Thus the illustration of* Mendelian inheritance is inconclusive Besides the numbers were too small

We have noticed elsewhere that crossing different breeds of pigeons often results in forms which more or less resemble the reputed original

ancestor the wild rock dove in other words, reversions occur. Often however, the results seem quite anomalous which is probably due to the number of latent characters which different races of pigeons appear to carry

Mice.—Mendelian phenomena have been carefully studied in mice Thus when a grey mouse is paired with an albino the hybrid offspring are always grey. When these are inbred they yield greys and albinos approximately in the proportion of 3 : 1. Thus Cuenot obtained 198 grey and 72 albinos

Darbishire has obtained many results which harmonise well with Mendelian theory while others require some ingenuity if they are to be fitted in with this interpretation. As a good case we may cite one where the inbreeding of pigmented mice—derived from crossing pigmented and albino individuals—yielded 159 pigmented young and 55 albinos (53.5 being the theoretical anticipation) When similar hybrids were paired with pure albinos they yielded 69 pigmented and 69 albino forms precisely as the theory would lead us to expect



Cuénot crossed an albino AG (with latent grey) with an albino AB (with latent black) and obtained albinos (AGAB). He crossed a black mouse CB with an albino AY (with latent yellow), and obtained yellow mice (CBAY) He then paired AGAB (albino) with CBAY (yellow) and obtained 151 young—81 albinos 34 yellow, 20 black 16 grey the theoretical anticipation being —76 albinos 38 yellow 19 black 19 grey. This is an exceedingly striking and convincing case

Waltzing mice.—The mice of this interesting Japanese breed have among other peculiarities the habit of waltzing round in circles When waltzing mice are crossed with normal mice their abnormal quality behaves as a recessive

Guinea-pigs.—If a black guinea pig of pure race be crossed with a white one the offspring will be all black, and if these are mated with each other the recessive white character reappears on the average in one in four of their offspring. These whites mated with each other produce only white offspring while the black are as usual of two kinds pure blacks and impure blacks. Similarly, as Professor Castle has shown, a rough coat is dominant over a smooth coat, and a short coat over a long coat.

Rabbits.—Hurst paired white Angora rabbits (with pink eyes and silky hair) with "Belgian hare" rabbits (with pigmented skin dark eyes, and short yellow fur). The hybrids were pigmented like the "Belgian hares" but the fur was grey like that of the wild rabbit. These hybrids were inbred, and 14 distinct types resulted—an apparent "epidemic of variation" to which Mendel's theory has supplied the clue for four pairs of contrasted characters are involved in the hybrid inbreeding—namely, short hair versus long hair pigmented coat versus albinos grey versus black coat, uniform versus marked coat (Dutch marking latent in the albinos), and the 14 distinct types illustrate the possible combinations.

As regards short hair versus long hair, Hurst found that when the short-coated hybrids were inbred they produced short haired forms like the Belgian hare grandparent, and long haired forms like the Angora grandparent. Out of 70 which reached the age of two months or more 53 were short haired and 17 long haired—a close approximation to the Mendelian anticipation 52.5 17.5. Similarly as regards pigmented coat versus albino the hybrids, when inbred yielded 132 pigmented and 39 albino forms—a close approximation to the Mendelian expectation, 129 43 and so on.

Cats.—There are some interesting results as to colour (Doncaster). Thus "pure orange ♀ crossed by pure black ♂ gives tortoiseshell females and yellow males but black crossed by orange gives black males or females tortoiseshell females and orange males. It seems that orange usually dominates over black in males while in females the orange (for some unknown reason) is less dominant and tortoiseshell results. Male tortoiseshell cats are very rare. In this case the results are complicated by some peculiarity wrapped up with sex.

When a male tortoiseshell is paired with a female tortoiseshell the kittens are tortoiseshell orange and black—which is what Mendelian theory would lead us to expect.

Man.—Evidence of Mendelian phenomena in man is as yet very scanty. It appears that the condition known as brachydactylism

where the fingers are all thumbs with two joints instead of three, is dominant over the normal In five generations chronicled by Farabee about half of the offspring were of the abnormal type, though the marriages were apparently always with unrelated normal individuals Moreover no normal member of the lineage is known to have transmitted the abnormality Another good case has been recently discussed by Drinkwater

Of great interest also is Mr Nettleship s account of the descendants of one Jean Nougaret (born 1637) who was afflicted with 'night blindness' —a condition apparently due to loss of visual purple It seems to behave like a unit character There are records of over 2,000 individuals and the night blindness is dominant over normal eyesight The notable point is that during two and a half centuries no normal member of the lineage who married another normal, whether related or not, ever transmitted the disease

Human eye colour affords another illustration. It is largely determined by the presence or absence of two distinct layers of pigment In the true blue eye only one of these pigmentary layers is visibly present, the posterior purple pigment of the choroid which being reflected through the fibrous structure of the iris produces the blue colour In the absence or partial absence of this pigment the eye appears to be 'pink, as in albinos In the ordinary brown eye two layers of pigment are present, for in addition to the posterior purple layer there is also an anterior brown layer, in front of the iris Major C C Hurst found that the eye with two layers of visible pigment (duplex) is dominant and the eye with one layer of visible pigment (simplex) recessive Or, putting it in another way the presence of the brown front layer is dominant to its absence Practically the same conclusion was reached independently by Professor and Mrs Davenport

The Davenports and Major Hurst have also brought forward some evidence illustrating in typical Caucasians the dominance of dark to fair skins, their segregation in the same family and the apparent purity of the extracted fair individuals Hurst also gives evidence that fiery red hair behaves as a recessive to brown and that the musical sense or temperament is also recessive It seems as if an individual is non musical owing to the presence of an inhibitory factor preventing the expression of musical temperament which is potentially present in everyone (Hurst 1912)

It would be interesting to have precise information as to the progeny of Eurasians who intermarry, for here the original hybrids result from the mixture of two very distinct races

CHAPTER XIX

THE FACTOR HYPOTHESIS AS APPLIED TO PLANTS

JOHN M COULTER AND MERLE C COULTER

Thus far we have been considering Mendel s law in its simple form and have enlarged but little upon Mendel s original statement The value of the law is apparent Upon its republication in 1900 it was taken up by biologists and numerous breeders set to work to test it As a consequence data for and against it began to accumulate. As might be expected there was much apparent evidence against the law but as geneticists developed a better conception of the mechanism the contradictory evidence was explained away Almost every type of inheritance has now been explained according to Mendel s law Some of the explanations are very complicated and cannot be included in this presentation A few of the more important cases however will be presented

I PRESENCE AND ABSENCE HYPOTHESIS

This may be regarded as a new method of Mendelian thought. It was first suggested by Correns but later was worked out in detail by other geneticists especially Hurst, Bateson Shull and East It is merely a modification of the mechanism involved For example in the case of a hybrid obtained by crossing tall and dwarf parents the result had been explained as due to the fact that one chromosome bears a determiner for tallness and the other one of the pair carries the determiner for dwarfness In other words each one of a pair of allelomorphs is repre ented by a determiner two determiners thus being present Dwarfness in this case would be the result of the interaction of that determiner and its environment during the development of the body and the ame for tallness When both were present however, the conception of the situation was as follows The determiner for dwarfness setting up its usual series of reactions early became paralyzed by the determiner for tallness or its products This re ult was called the dominance of the character for tallness It was as if the determiner for tallness completely prevented the activity of the determiner for dwarfness This conception was apparently borne out

by the facts and was the explanation of the mechanism generally accepted

According to the presence and absence hypothesis however the situation is looked at from an entirely different point of view Tallness is the result of a determiner but dwarfness is merely the result of the absence of the determiner for tallness The dominant character is produced by an inheritable determiner but the recessive character appears only when the dominant determiner is lacking This conception has some evident advantages and may modify the previous Mendelian diagram as shown in Figure 58 This appears to be a simpler mechanism to account for the phenomenon called dominance In the case of the dwarf form there is a normal course of development, in the case of the tall parent or hybrid however an additional determiner

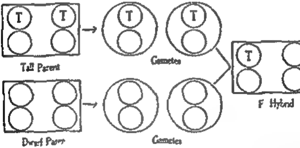


FIG 58—Diagram showing how the original scheme must be modified to satisfy the presence and absence hypothesis (From Coulter and Coulter)

stimulates cell growth or cell division or both It is a simpler and more useful conception so long as it fits the facts Some investigators however claim that it cannot be applied to all the situations that have been discovered

[It should be emphasized here that the word determiner as used in the foregoing paragraphs is not synonymous with the word gene A recessive character is not due to the absence of a gene but merely to the absence of something that is present in the dominant gene In this form the presence and absence idea is acceptable]

Additional advantages of the presence and absence hypothesis will appear in connection with a consideration of blending inheritance and of cumulative factors in inheritance Attention however should be called to the fact that those who accept the presence and absence

hypothesis do not use the form of notation thus far used in explaining Mendelian inheritance Assume that *T* is used to express the determiner for tallness its same letter (*t*) is used to express the absence For example instead of using *D* for dwarfness *t* is used for lack of tallness (Fig 59) It is a matter of convenience to have a symbol to represent the recessive the absence of something that is present in another individual

In summary the essential difference between the presence and absence hypothesis and that of dominant and recessive is that in the former case the recessive determiner has no existence at all while in the latter case it exists but is in a latent condition when associated with the dominant

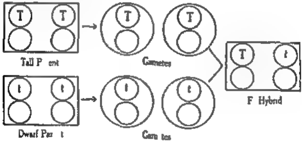


FIG 59—Diagram showing how presence and absence scheme is actually used with small letter representing absence (*From Coulter and Coulter*)

II BLENDS

This type of inheritance when first discovered was thought to be in direct conflict with Mendel s law It is a case in which dominance seems to fail for the two alternative characters both express themselves and the result is an average between them It is easy to explain this situation in accordance with the presence and absence hypothesis without any violation of Mendel s law

The classic example of blending inheritance was presented by Correns in breeding work upon *Mirabilis Jalapa* the common four o clock Correns crossed red and white varieties and all the hybrid progeny had rose pink flowers This was a color blend distinctly intermediate between the colors of the two parents The F generation therefore seemed to contradict Mendel s law in that one color character was not completely dominant over the other The real situation however appeared in the F generation obtained by inbreeding

individuals of the F generation which showed the blend. By in breeding the pink hybrids Correns obtained the perfect 1 2 1 ratio that 1 red like one grandparent 2 pink like the hybrid parent, and 1 white like the other grandparent. Segregation was evidently taking place the only unusual thing being the *appearance* of the F individuals and that was explained immediately as failure of dominance (see Fig 60)

The question this introduces therefore is that of a mechanism which could account for such a result. The easiest explanation offered is that the red parent was a homozygote for redness (double dose) and the hybrid a heterozygote (single dose), the inference is that

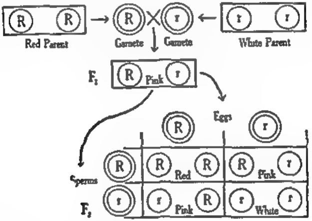


FIG 60—Diagram illustrating blending inheritance discovered by Correns in *Mirabilis jalapa* (*From Coulter and Coulter*)

a single dose produces pink while a double dose produces red. A theoretical explanation of this occasional difference in the result of double and single doses is as follows. Imagine that the body cells of a plant have a certain capacity for expressing hereditary characters. In such a case just as a given quantity of solvent can dissolve only a given amount of solute so the body cells can express hereditary characters only to a definite limited extent. In the four-o clock a single dose of redness may be thought of as half saturating the body cells, while a double dose completely saturates them. In cases showing complete dominance however a single dose completely saturates the cells and a double dose can do nothing more. This analogy assists in visualizing on the one hand the necessary mechanism of blends (apparent failure

of dominance) and on the other hand that for cases of complete dominance

Another example of simple blending inheritance is the case of Adzuki beans described by Blakeslee In this bean the mottling of the seed coat is dominant to the lack of mottling In the hybrid condition however, the mottling is lighter than in the pure or homozygous condition Heterozygous plants therefore can be easily distinguished from homozygous plants so that the 1 2 1 ratio is evident on external inspection rather than the usual 3 1 ratio

III THE FACTOR HYPOTHESIS

Mendel concluded that each plant character depends upon a single determiner Inheritance however has proved to be a much more complex phenomenon than indicated by Mendel s peas Ratios have appeared that were puzzling and geneticists were forced to the conclusion that there may be a compound determiner for a single character This conception is called the *factor hypothesis* and the growing complexity of genetics has developed in connection with this hypothesis With the consideration of *factors* instead of *determiners* one passes from elementary to advanced genetics Previously we have used the word determiner implying Mendel s idea that a single determiner is responsible for the development of a plant character and this has been true of the examples of inheritance previously considered It is understood now however that a character is frequently determined by the interaction of two or more separately heritable factors and hence the factor hypothesis The distinction between factors and determiners should be made clear In case only one factor is involved in determining a character there is no distinction between factor and determiner and in such a case the term factor should not be used

1 Complementary factors —This is the simplest expression of the factor hypothesis and it may be illustrated by some of East s work Crossing red grained and white-grained corn he obtained all red in the F generation This would suggest that the F generation would show 3 red to 1 white but it showed 9 reds to 7 whites which did not suggest Mendelian inheritance It is in accord with Mendel s law however if we consider that two complementary factors are necessary to produce the red character and that each of these factors is inherited separately Such a situation would give a dihybrid ratio as indicated in Fig 61 It will be seen that out of 16 progeny 9 will be red for they alone contain the complementary factors the other 7 will be white

The situation is thus explained by the dihybrid ratio, but although only one character is involved that character depends upon two complementary factors

Another situation is worth noting No 6 of the diagram is white because it contains only one of the necessary factors, No 11 is white

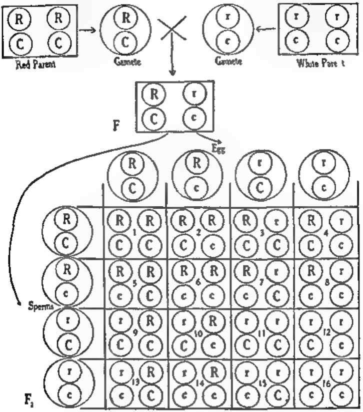


FIG 61 —Diagram illustrating behavior of complementary factors in cross between red grained and white grained corn *R* and *C* must both be present to produce red-grained corn (*From Coulter and Coulter*)

for the same reason but its germinal constitution is just the opposite What would happen if these two are crossed? There is only one possibility since each is a homozygote producing only one kind of gamete The result would be red and thus a cross between two whites would produce only reds What would happen from crossing Nos 6 and 15 the former being a homozygote and the latter a heterozygote?

It is obvious that the resulting progeny would be one-half white and one-half red although both parents are white The same result would be secured in crossing Nos 11 and 14 A cross between Nos 14 and 15 both of which are heterozygotes would result in 3 whites and 1 red the ordinary 3 1 ratio These illustrations show how differently the same phenotype may behave in inheritance In each case two whites were crossed that is the same phenotypes but three different ratios were obtained because the genotypes were different

The striking feature of this situation is that one can cross two whites and get a red This gives an insight into the so-called phenomenon of *reversion* For example in the course of numerous breeding experiments Bateson obtained two strains of white sweet peas each of which when normally 'selfed bred true to the white color but when these two were artificially crossed all the progeny had purple flowers like the wild Sicilian ancestors of all cultivated varieties of the sweet pea This appeared to be a typical case of reversion Further breeding however showed that this was just such a case of complementary factors as we have been considering One of Bateson s white strains had one of the factors for purple and the other strain had the other factor

Complementary factors have been defined and the method of their inheritance described but is there any mechanism to explain the situation? A suggestion may be obtained from plant chemistry The most prominent group of pigments in plants is the group of anthocyanins which are produced as follows Plants contain compounds called chromogens which are colorless themselves but which produce pigments when acted upon by certain oxidizing enzymes or oxidases This is a sufficient mechanism for the behavior of complementary factors If one of East s white strains of corn contained a chromogen capable of producing red but lacked the necessary oxidase it would remain colorless If the other white strain contained the oxidase but no chromogen it would remain colorless In crossing them however chromogen and oxidase would be brought together and a red grained hybrid would be the result Inbreeding such red grained individuals of course would give red and white progeny in a ratio of 9 7 as explained in connection with East s corn This seems to be the explanation of the behavior of complementary factors in many cases of color inheritance

Where other characters are involved the mechanism must be somewhat different In some cases the two factors may be the enzyme

and the compound the enzyme attacks as in the oxidase and chromogen situation just described On the other hand, we might be dealing with two chemical compounds that are inert when occurring separately but active when brought together active in such a way as to produce a distinctly new character Also two active substances might neutralize one another when brought together in a hybrid and the failure in their activity might result either in a new character or the failure of some parental character to develop Such are some of the possible mechanisms to explain the behavior of complementary factors

Hybridizing therefore is much like mixing chemicals in a test tube We know that very wide crosses cannot be made successfully but the surprising thing is that certain very close crosses are constantly unsuccessful even though both parents may cross freely with closely related types We obtain a glimpse of the possibility of such apparently inconsistent behavior when we consider the chemical possibilities suggested by the behavior of complementary factors

The origin of complementary factors is an interesting field of speculation Did they originate together or separately? A natural inference would be that they originated together for neither would be of any use without the other It should be remembered however that the idea of use as explaining the occurrence of everything in a plant is being abandoned one must think rather of a plant as a complex physico-chemical laboratory No one claims that all chemical reactions are useful they are simply inevitable and plant characters are the result of chemical reactions and physical necessities Even though we assume the simultaneous origin of two complementary factors they would have to be put on separate chromosomes for the factors are separately inherited

The other alternative is to suppose that these factors originated independently in the history of a plant In this case of course the first one to be produced would remain functionless until finally its complement came into existence This might be an explanation of what are called latent characters Also they might have not only originated independently but in different varieties or species In this case if natural hybridizing should bring them together the result would be the appearance of a new character, and this may have been a very important factor in the origin of species

This may serve as an introduction to the factor hypothesis with complementary factors as an illustration simply because it is the simplest situation There are many other kinds of factors recognized

but we shall not attempt to list all of the proposed types A simple illustration of the better known types is as follows

a) A *complementary* factor i added to a dissimilar factor to produce a particular character

b) An *inhibitory* factor prevents the action of some other factor

c) A *supplementary* factor is added to a dissimilar factor with the result that the character is modified in some way

d) A *cumulative* factor when added to another similar factor, affects the degree of development of the character

Some examples of these types will make them clear, those for complementary factors having been given previously

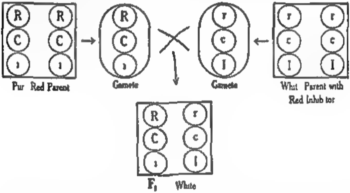


FIG 62 —Diagram illustrating behavior of inhibitory factor (*From Coulter and Coulter*)

2 Inhibitory factors —Recalling East s experiment with red grained corn it will be remembered that when both factors for red were present the grain was red, but when either factor was absent the grain was white Later he crossed these strains with a new white strain and the result was surprising The pure red strain produced gametes carrying both the red factors and it would be expected that whatever such a gamete mated with would result in red progeny but when this pure red was crossed with the new strain of white the progeny were all white although the hybrids certainly contained both factors for red The explanation which first occurred to East and which later experiments confirmed, was that the new white strain contained an inhibitory factor, which prevented the development of red even though both the complementary factors for red were present

Figure 62 illustrates the situation and shows why all the individuals of the F generation are white It is interesting to note further the possibilities of white and red in the F_2 generation They would be

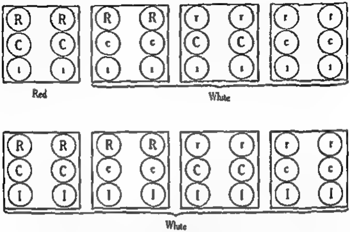


FIG 63—Diagram showing some possible combinations in F when F of Figure 62 is inbred Individual on left end of upper set red grained because *R* and *C* both present and *I* absent other individuals in upper set white because lacking *C* or *R* or both individuals in lower set with inhibitory factor and therefore white whatever other combinations of factors they may contain (*From Coulter and Coulter*)

numerous since we are dealing with trihybrid ratios (see Fig 63) This does not exhaust the possibilities for the cases given were homozygotes each producing a single kind of gamete There remains for consideration the heterozygote situation (see Fig 64)

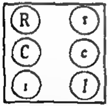


FIG 64—(*From Coulter and Coulter*)

The possible mechanism of the inhibitory factor is as follows We have assumed that red is produced only when the enzyme is present to oxidize the chromogen Enzymes are very sensitive their activities may be affected or completely checked by various agents Suppose that *I* of the diagram be such an agent and the necessary mechanism is apparent When *I* is present *R* is paralyzed, so that it cannot oxidize *C*

3 **Supplementary factors**—A supplementary factor is one that is added to a dissimilar factor with the result that a character is modified in some way

In his work upon red grained races of corn East found occasionally a few purple grains His conception of the situation is as follows The pure red plant contains two complementary factors one (C) a chromogen and the other (R) an enzyme which when brought together produced the red color The purple grains however must be explained by the presence of still another factor (P) the resulting situation being represented in Figure 65 Of course when C is absent no pigment whatsoever can be produced As a consequence we will assume that the presence of C is constant and that P and R are variables For a similar reason we will assume that the absence of I is constant The figure shows three possibilities from which the following conclusions may be drawn (1) when P and R are both present the result is purple grains (2) red appears only in the absence of P (3) P although present will not develop any color in the absence of R

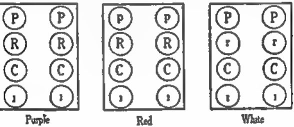


FIG 65—Diagram illustrating action of supplementary factor (*From Coulter and Coulter*)

This is a typical case of a supplementary factor that is one which is added to a dissimilar factor with the result that the color character is modified The mechanism of this situation will make clearer the behavior of the supplementary factor If C is the chromogen and R the enzyme what is P? The suggested answer can be obtained from plant chemistry It is found that the purple pigment is produced by the same substance as the red but represents a higher state of oxidation The conclusion is obvious C is oxidized by R up to a certain point where red is produced but if P is also present it represents an additional enzyme which attacks the red pigment and oxidizes it still further into purple P is incapable of attacking the original chromogen but when R carries the attack to a certain point, P can function and carry the oxidation further As a consequence P without R gives white grains while R gives red grains only in the absence of P

4 **Cumulative factors** —These will be considered under the next heading, "Inheritance of quantitative characters"

In addition to the four types of factors given, the literature of genetics also contains discussions on intensifying factors diluting factors distribution factors etc. These however, do not introduce any new mechanisms

5 **Inheritance of quantitative characters** —This phase of the factor hypothesis if true is of fundamental importance not only to genetics but to general biology. It is based upon the conception of cumulative factors and as it is presented it will be realized that it throws light not only upon numerous breeding experiments but also upon variation in general which means evolution also. A cumulative factor was defined as one which when added to another similar factor, affects the degree of development of the character

It will be recalled that Correns crossed red and white strains of *Mirabilis* and obtained pink hybrids. The suggested explanation of this result was that a single dose of the red determiner gives pink while a double dose gives red. When Correns inbred these pink hybrids he obtained the result presented in Figure 60 that is 1 red, 2 pink 1 white. This result is obvious and the mechanism is plain

With this diagram in mind we shall consider some of the experiments of Nilsson Ehle at the Swedish Experiment Station. He crossed two strains of wheat with red and white kernels. The F_1 individuals had light red kernels which of course suggests a repetition of the situation shown by *Mirabilis* in the experiment of Correns. The F_2 generation however showed a very different result. The reds and whites appeared in the ratio of 15 1 but in addition to this among the 15 reds there could be distinguished varying degrees of redness. Nilsson Ehle suspected that 15 1 meant a dihybrid ratio 16 individuals being necessary to give the ratio so that he constructed the tentative scheme shown in Figure 66

This shows a regular dihybrid ratio except that the two factors involved are similar. Applying the single dose and double dose conception as used in the case of Correns pink *Mirabilis*, we reach the following conclusions. No 1 only has four doses and therefore it only is deep red, Nos 2 3, 5, 9 have three doses and are somewhat lighter red. Nos 4 6 7, 10 11 13 have two doses and are still lighter red. Nos 8 12, 14, 15 have one dose and are very light red, while No 16 alone has no dose and is the only pure white. This accounts for the 15 1 ratio and the different shades of red. This is entirely in

accord with the conceptions that have been presented and only two assumptions are necessary (1) that dominance is absent and two doses have twice the effect of one (2) that the independent similar factors are cumulative in their operation, and are paired with their absence in the hybrid This was Nilsson Ehle s conception and of

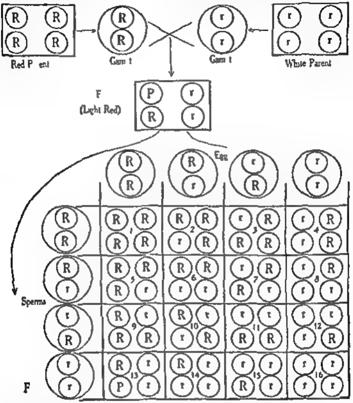


Fig 66 —Diagram illustrating Nilsson Ehle s explanation of 15 1 ratio obtained in F generation from cross between red-grained and white grained wheat (*From Coulter and Coulter*)

course he tested it by further experimental work the results consistently confirming the conception

Since it is important to fix this conception clearly in mind another type of diagram may represent the facts even more clearly The proportion of individuals showing the various degrees of redness in the F is graphically recorded in Figure 67 each dot representing one dose of the factors in question

Continuing these investigations Nilsson Ehle next discovered a new strain of red grained wheat which when crossed with the pure white strain yielded F_1 hybrids of intermediate intensity of red as before The F_2 generation however showed a different situation Reds and whites were obtained in the proportion of 63 1 the 63 reds as before falling naturally into different groups on the basis of degree of redness Applying the same conception as before Nilsson Ehle

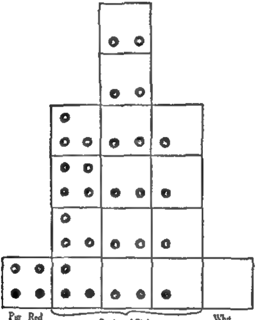


FIG 67 —Another method of visualizing Nilsson Ehle s 15 1 ratio (see Fig 66) (*From Coulter and Coulter*)

discovered that in this case he was dealing with a trihybrid situation Without constructing the usual Mendelian diagram which would have to be extensive enough for 64 individuals the situation as it appeared in the F generation may be represented by Figure 68 If the graph is surmounted by a curve we recognize the regular probability curve exactly the kind of curve biometricians use to represent the fluctuating individuals about a specific type

This conception of cumulative factors therefore has far reaching significance For a long time biologists have recognized individual

variation within the species; Darwin depended upon it as the basis of his theory of natural selection as the origin of species; in fact, ever

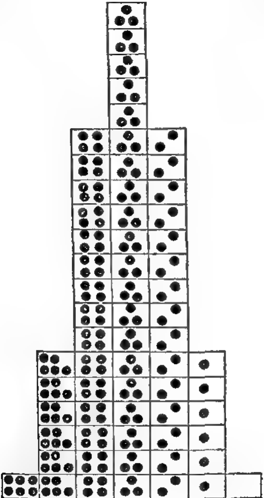


FIG. 68.—Diagram illustrating Nilsson-Ehle's 63 : 1 ratio. (*From Coulter and Coulter.*)

since Darwin's *Origin of Species* individual variation has been fundamental in our conceptions. To account for this universally recognized phenomenon Darwin proposed his *transportation hypothesis* as

a possible explanation which as will be recalled, did not long survive Weismann offered in explanation his *germinal selection* which was soon discarded because it was beyond the possibility of experimental testing Aside from these two attempts to explain individual variation no other comprehensive scheme had been presented Biologists had simply recognized the fact of individual variation without any conception of the mechanism. They knew that individual variation existed but had even stopped asking why it existed

The importance of this new theory therefore is obvious It is an ingenious explanation of the inheritance of quantitative characters and of the existence of individual variations Furthermore the theory has not been developed through meditation but has its basis in scientific experiments It is imaginative to a certain extent of course as is every other valuable theory, but unlike most such theories it has a substantial foundation namely, Mendel s law

CHAPTER XX

THE FACTOR HYPOTHESIS AS APPLIED TO ANIMALS

Immediately after the announcement by De Vries in 1900 of the rediscovery of Mendel's paper zoologists in Europe and in America began experiments in animal breeding with the idea of discovering to what extent Mendel's laws were applicable It was soon found that the principles of unit characters dominance segregation monohybrid dihybrid and trihybrid ratios were of practically universal application A number of instances of Mendelian heredity in animals have already been presented in the preceding chapter and no more simple Mendelian cases need be described For a considerable period the animal breeders proceeded no farther in their analysis of the mechanism of heredity than Mendel had done so many years before In time however new facts came to light that needed further analysis and the older Mendelism was superseded by neo-Mendelism This new phase in the study of heredity is in the forefront of interest today Neo-Mendelian heredity in plants has already been discussed It remains for us to present the data on some phases of neo-Mendelism in animals

ILLUSTRATIONS OF THE FACTOR HYPOTHESIS

THE FACTORIAL ANALYSIS OF COLOR IN MICE

Miss Durham after extensive breeding experiments with numerous strains of differently colored mice has been able to show that the appearance of a particular color in an individual mouse is dependent upon the presence or absence of several independently inherited factors evidently represented by genes in as many different chromosomes It seems possible to classify these factors as follows

B = black pigment, which masks chocolate pigment
b = absence of B which gives chocolate

I = intensity factor
i = absence of intensity or dilution factor

C = a complementary color factor acting with P
P = a complementary pigment factor acting with C

If either C or P is absent, albino mice result no matter what other color factors may be present

The factorial make up of the various mice in Miss Durham s experiments would then be represented as follows

$BICP$ = black
$BiCP$ = blue (dilute black)
$bICP$ = chocolate (absence of black)
$biCP$ = silver fawn (dilute chocolate)

The following experiments indicate the mode of heredity on the factorial basis

1 P Black ($BICP$)×Silver fawn ($biCP$)
F 100 per cent Black ($BICP$ $biCP$)
F Black ($BICP$) Blue ($BiCP$) Chocolate ($bICP$) Silver fawn ($biCP$)

Black	Blue	Chocolate	Silver fawn
9	3	3	1

2 P Blue ($BiCP$)×Chocolate ($bICP$)
F_1 100 per cent Black ($BiCP$ $bICP$)
F_2 Black ($BICP$) Blue ($BiCP$) Chocolate ($bICP$) Silver fawn ($biCP$)

Black	Blue	Chocolate	Silver fawn
9	3	3	1

3 P Blue ($BiCP$)×Silver fawn ($biCP$)
F 100 per cent Blue ($BiCP$ $biCP$)
F_2 Blue ($BiCP$) Silver fawn ($biCP$)

Blue	Silver fawn
3	1

DIFFERENT KINDS OF ALBINOS

Any one of the color types mentioned if lacking in the factor C will be an albino though carrying the other factors for color For example there may be a Black albino ($BIcP$) a Blue albino ($BicP$) a Chocolate albino ($bIcP$) or a Silver fawn–albino ($bicP$)

That color factors are present in albinos may be shown by the following experiment An albino had appeared in a Black stock and was crossed with a Silver fawn thus

4 P Silver fawn ($biCP$)×Albino extracted from Black ($BIcP$)
F_1 100 per cent Black ($biCP$ $BIcP$)

F

Black ($BICP$)	Blue ($BiCP$)	Chocolate ($bICP$)	Albino Black ($BIcP$)	Silver fawn ($biCP$)
27	9	[illegible]	[illegible]	3

Albino Blue ($BicP$)	Albino Chocolate ($bIcP$)	Albino-Silver fawn ($bicP$)
3	3	1

The ratios given are the theoretical ratios for a trihybrid Mendel ian experiment and the actual results have closely approximated these As a matter of fact sixteen albinos appeared and it is not possible except by breeding to tell one kind from another Breeding each with for example Silver fawn would readily reveal the differences for the F generation would all be of the color that is masked by the lack of *C* in these albinos In the language of Johanssen there is only one albino *phenotype* but there are four albino *genotypes* Similarly in experiments (1) and (4) which have just been described the indi viduals are all Black (phenotypically identical) but that they are not genotypically alike is clearly shown by inbreeding them In experi ment (1) we get only individuals of the four color types while in experiment (4) we get in addition to the four color types four albino types

FACTORIAL ANALYSIS OF COAT COLOR IN SWINE

Some breeds of swine have a red coat color as the Duroc Jerseys Other breeds have a sandy yellowish color Still others are white There are other colors but they may be ignored for present purposes Wentworth has shown that there are two genotypically distinct though phenotypically identical sandy types the factor analysis being as follows

$$SSTT = \text{red}$$
$$SStt = \text{sandy}$$
$$ssTT = \text{sandy}$$
$$sstt = \text{white}$$

If this analysis be correct when the two different sandy genotypes (*SStt* and *ssTT*) are interbred the result would be as follows All of the F individuals would be red These when interbred give the fol lowing F phenotypic ratio

$$9\ ST = \text{red}$$
$$3\ St = \text{sandy}$$
$$3\ sT = \text{sandy}$$
$$1\ st = \text{white}$$

The phenotypic ratio is therefore 9 red to 6 sandy to 1 white which is a rare modification of the 9 3 3 1 dihybrid ratio and is due to the fact that the phenotype sandy, consists of two different genotypes in equal numbers

COAT COLORS IN GUINEA PIGS

In guinea pigs the wild type coloration is a kind of reddish gray mixture called "agouti There are also black coat colors and whites (albinos)

Agouti when crossed with some types of white gives all agouti in the F generation and 3 agouti to 1 white in the F generation A black guinea pig crossed with agouti gives all agouti in the F and 3 agouti to 1 black in the F generation Evidently both black and white are recessives to agouti so agouti must be due to at least two dominant color factors A and C

If we assume that A is a dominant factor whose recessive allelomorph a gives black color and that C is a dominant factor whose recessive allelomorph c gives white color then we may put down the formulas for the genetic composition of the three coat colors as follows

$$AACC = \text{agouti}$$
$$AAcc = \text{albino (of one kind)}$$
$$aaCC = \text{black}$$

Then when black ($aaCC$) is crossed with white ($AAcc$), all of the F generation would be agouti and the F ratio would be as follows

$$9\ AACC = \text{agouti}$$
$$3\ AAcc = \text{white}$$
$$3\ aaCC = \text{black}$$
$$1\ aacc = \text{white}$$

This would give a phenotypic ratio of 9 agouti to 3 blacks to 4 whites another rather slight but unusual modification of the familiar 9 3 3 1 ratio due to the fact that the phenotype white consists of two genotypes

Characters that seemed quite simple at first have been found by methods similar to those here presented to be complex when subjected to analysis Such apparently simple characters as human eye color and hair color though never fully analyzed would doubtless amply repay investigation If we knew as much about these characters as we do about some animal characters the testimony of a geneticist in a paternity case would be more valuable than it is at present

CHAPTER XXI

REVIEW OF MENDELISM

At this point it seems well to pause and to take stock of what we have learned about heredity by following Mendel's lead Let us first enumerate some of the rules or laws of heredity discovered by Mendel These are commonly known as *Mendel's laws*

Mendel's first law the law of dominance—When two parent types differing from each other with reference to a single unit character are crossed, the 'hybrid character resembles that of one of the parent forms so closely that the other either escapes observation completely or cannot be detected with certainty The character that appears in the first generation hybrids is called dominant' and that which apparently becomes latent is called recessive The law of dominance has been shown to be far from universal in its application In fact complete dominance is relatively rare and almost entire lack of dominance is not uncommon Evidently then dominance is not an essential feature of Mendelian heredity

Mendel's second law the law of segregation or purity of gametes—While the body cells and the germ cells of the F parent prior to the reduction divisions involved in gamete formation contain the determiners (genes) of both alternative characters and are therefore hybrid in character a segregation of the alternative genes (allelomorphs) takes place during maturation so that only one or the other gene comes to be present in any gamete Thus gametes are pure for any gene A gamete has one or the other of a pair of allelomorphs and is never hybrid with reference to any single character This law is by far the most important of Mendel's discoveries In fact it might be called *the* discovery of Mendel for it is almost unsurpassed among biological generalizations on account of its far reaching applicability The law has sometimes been called the *law of the splitting of hybrids* Whether dominance is present or not the law of segregation always holds The second law therefore is much more important than the first

Mendel's third law the law of independent assortment of differ

ent allelomorphs —To use Mendel s own expression ' the relation of each pair of different characters in hybrid union is independent of the other differences in the two original parental stocks ' This third law is only discoverable when we try to follow the assortment and recombination of at least two pairs of allelomorphs up to the second hybrid generation (F) If each allelomorph be studied by itself it will show nothing more than the facts indicated in the first two laws but as soon as we try to follow the modes of inheritance of more than one character simultaneously we find that we are merely dealing with the independent shuffling and assorting of two or more genes The way in which we explain the third law is that all genes that exhibit independent assortment are located in different chromosomes If two allelomorphs were in the same chromosome it is obvious that their association with each other in heredity would be much closer than if they were in different chromosomes Remember this when we come to consider a later proposition called *linkage*

Mendel's fourth law the law of recombination —According to Mendel this law means that the constant characters which appear in the several varieties of a group of plants (or animals) may be obtained in all the associations which are possible according to the mathematical laws of combination The genes carried by the chromosomes are shuffled about like a pack of cards and dealt out in all possible combinations according to the laws of chance The result of this is that the particular deal or hand that happened to be possessed by the parent is likely not to be repeated in any of the offspring if the number of differences involved is at all large Of course if there is only one point of difference between the two parents the character of the parent will be repeated in one out of each four individuals of the F_2 generation If there are two pairs of allelomorphs concerned, there will be one in sixteen in the F with the same combination as each original parent if three pairs of allelomorphs, one in sixty four if four pairs one in two hundred fifty six if ten or more pairs one in hundreds of thousands or millions Nearly all human beings differ from one another with regard to hundreds of allelomorphs Is it not remarkable then that there is as much resemblance between two brothers as there sometimes is? This condition will be better understood when we come to discuss the limitations of the law of independent assortment which Mendel failed to discover and which is explained by the law of linkage

The concepts expressed in the above laws may be considered to have originated with Mendel It must be remembered however that

Mendel had no knowledge of chromosomes or of the chromosomal mechanism of maturation which now seems to be the machine responsible for the regularities seen in the various Mendelian ratios and for segregation in general It is remarkable therefore that Mendel foresaw a mechanism within the genetic apparatus of plants that coincides in principle with that subsequently discovered Among the great discoveries that have resulted from the use of Mendelian methods and procedures are the factor hypothesis the chromosome theory of heredity and of sex determination linkage and crossing over and the finer details of the heredity machine

The presence and absence theory —In its original form the presence and absence theory implied that some gene was present in the dominant individual that was absent in the recessive It has been discovered however that this theory fails to hold especially in cases of multiple allelomorphs and probably does not hold at all As an example of multiple allelomorphs we may cite the various eye-color mutants of *Drosophila* (see page 294) A whole series of eye color conditions ranging from red to white are all known to be the result of mutational changes in the same gene with red the wild type condition being dominant over any of the mutant conditions Now these various colors such as vermilion pink salmon cream etc are all recessive to red but dominant over white This shows that the gene for eye color is present in all these mutants but is merely modified in various ways or in varying degrees

The presence and absence hypothesis therefore might then be stated as follows There is some positive element present in the dominant gene that is absent in the recessive allelomorph which prevents the recessive gene from expressing itself In this form the theory is rather helpful and serves to rationalize the practice now universal of representing any dominant gene by a capital letter such as *A* and the recessive gene by the equivalent small letter *a*

The factor hypothesis —Mendel believed that for each character there was a determiner that each determiner produced a character unaided According to the factor hypothesis as we have seen such simple characters as colors in plants and animals depend upon the interaction of several genes which are called factors because they are not single causes but merely co operative agents It is now coming to be believed that each character of the organism is the product of the interacting of many possibly all of the genes in the organism but that some of the genes affect a given character more than do others

It remains to be discovered to what extent each character is the result of the interaction of all the genes When once we learn that a single character may depend upon the interaction of two or more independently inherited and segregating factors or genes it becomes possible to understand all sorts of puzzling and apparently non Mendelian ratios The adoption of the factor hypothesis has justified itself over and over again, for it has been the instrument that has led to a really scientific genetics and has served to bring under one category all sorts of hereditary phenomena that had formerly been considered fundamentally different Thus there is now no further need for the three categories of heredity alternative, blending and particulate All three are now seen to be phases of alternative, or Mendelian heredity Especially striking is the way in which the idea of *multiple factors* ("cumultative or "duplicate factors of some authors) has served to rationalize and to bring into line with other Mendelian phenomena the data about the *inheritance of quantitative characters* Another service of the factor hypothesis comes out in connection with the discovery of *lethal factors* There is a large number of genes or factors whose presence in the homozygous condition (i e when a given factor is present in both gametes that unite to form a zygote) leaves the individual derived from such a zygote lacking in something essential for life All such individuals in any breeding experiment will fail to survive, and their absence will be noted when the ratios of the various combinations are worked out The failure of a certain expected combination to appear in the F generation is attributed to the presence of a lethal factor in the stock It can readily be proven that many of the surviving individuals possess the lethal factor in a heterozygous condition having one dose of the normal allelomorph along with the lethal factor *These lethal factors can be identified and located as readily as* characters that actually appear The subsidiary hypothesis of lethal factors has had a far reaching influence upon some of the most advanced phases of modern genetic practice

CHAPTER XXII

SEX LINKED HEREDITY

Up to this point we have been dealing with Mendelian experiments in which no more than one gene in any given chromosome was concerned The various Mendelian ratios including the modified ratios presented in connection with the factor hypothesis depend upon each of the different *allelomorphic factors involved being in a different* pair of chromosomes If two or more genes were in the same chromosome one would not expect them to follow the laws of random assortment and random recombination The study of sex linked heredity opened the way to the discovery that particular genes are in particular chromosomes that they tend to remain together in heredity but that genes in homologous chromosomes are frequently exchanged in a mutual fashion This discovery has led to a knowledge of linkage and crossing over and to the discovery of the detailed architecture of the germ plasm

Nearly twenty years ago a peculiar kind of heredity known as sex linked heredity was discovered and explained by Morgan We had previously known of this kind of heredity in man as in the case of color blindness free bleeding etc but its mechanism was not even guessed at It had long been known that color blind individuals are almost invariably males that such males marrying normal women never have any color blind offspring but that their daughters when mated with normal men have some color blind sons but never color blind daughters Thus color blindness shows a strong predilection for males and is called a sex linked character Free bleeding night blindness and several other human characters are known to be inherited in the same fashion

The mechanics of this form of heredity was worked out by Professor T H Morgan as the result of his work on the classic fruit fly *Drosophila melanogaster* In this valuable little insect the eyes are typically bright red In a stock of typical red eyed flies Morgan one day noted one white eyed male This had been born of typical red eyed ancestry so the white eye character in addition to being sex linked was a *mutant* appearing suddenly without any preliminary steps To test the heritability of this new character the white eyed

male was mated to a normal red eyed female The offspring of this mating were all red eyed in appearance (phenotypically), but the females were obviously all genotypically hybrid red and white eyed for when mated with normal red eyed males half of their sons were white eyed and half red eyed but all daughters were red eyed Subsequent experiments showed that half of the daughters were pure red eyed and half hybrid red and white eyed Now what sort of mechanism in the germ cells could account for this peculiar but very uniform type of hereditary behavior?

Professor Morgan explained the whole thing in a beautifully simple way by assuming that the gene of the sex linked character was situated in the X chromosome of the mutant male for the male has but one X chromosome along with a Y chromosome (see Fig 53) In the reduction division of the germ cells of this individual two kinds of male gametes (spermatozoa) are formed in equal numbers one carrying the X chromosome with the white eyed gene and the other the Y chromosomes Now whenever a female gamete (egg) of the normal red eyed female used as a mate is fertilized by a sperm with the X chromosome an XX individual or female will result and all of these females will get the white eye gene along with the X chromosome from their white eyed father But whenever an egg is fertilized by a sperm with the Y chromosome a male will be produced and all of these will be red eyed because they get their X chromosome from their mothers Why are not these female offspring possessing the white eye factor white eyed? Because they have also inherited an X chromosome containing the red eyed factor from their mothers and red eye is dominant over white eye These red and white eyed hybrid daughters are now bred to normal red eyed males whose X chromosome carries the red eye factor The females will produce two kinds of gametes in equal numbers one with the X chromosome carrying the red eye gene the other with the X chromosome carrying the white eye gene, while the male will produce two kinds of gametes one with an X chromosome carrying the red eye gene and the other with only a Y chromosome Each kind of male gamete will unite equally often with each kind of female gamete and the result will be four kinds of zygotes in equal numbers one in which two red eyed X chromosomes come together and produce a pure red eyed female one in which a red eyed and a white eyed X-chromosome come together and produce a hybrid female one in which a red eyed X chromosome and a Y chromosome unite to produce a red eyed male and finally, one in which a white eyed

X chromosome and a Y chromosome unite to produce a white eyed male This is the detailed procedure followed by all sex linked characters of this sort and is shown diagrammatically in Figure 69

We have seen that white eyes seem to be purely a male character inasmuch as it does not seem to express itself in females even when present in the germ plasm Why is this not just a secondary sexual character like the differences in size and shape of the body that characterize the two sexes? The answer to this query is that if we perform the proper breeding experiment it is possible to transfer the white eye character to the female For example let us take one of the daughters of a white eyed male and mate her with a white eyed male The female is a hybrid carrying the white eye gene in one of her X chromosomes and the red eye gene in the other X chromosome She will produce equal numbers of gametes with the two eye color genes The male will also have two kinds of gametes one with a white eye bearing X chromosome and one with a Y chromosome Random pairing of the types of gametes of the two parents will produce four classes of individuals in equal numbers one female with a red eyed X and a white eyed X (phenotypically red eyed) one female with two white eyed X chromosomes and therefore white eyed one male with a red eyed X and therefore red eyed and one male with a white eyed X, and therefore white eyed It is clear then that the white eye character is not limited to one sex but merely closely linked to the male sex under normal breeding conditions All sex linked characters are recessive for were they dominant they would express themselves somatically when either one dose or two doses of the gene are present The reason why the character appears normally in males only is that males have only one X chromosome a situation which make it possible for any recessive gene located in the X chromosome to express itself The female however has always two X chromosomes and unless she inherits the recessive gene from both parents —a condition that would rarely occur in nature—she would always have the corresponding dominant character in one X-chromosome to mask or offset the recessive character in the other X chromosome In man it is also the unfortunate male that falls heir to all of the rather detrimental sex linked characters while the female though inheriting the character more often than the male practically never shows the effects of it

An interesting variant upon the usual type of sex linked breeding experiment is the so-called *reciprocal cross* starting out with a white

eyed female derived from such an experiment as that just described and breeding her to a normal red eyed male. The F hybrids will be white eyed males and red eyed females the two eye colors simply changing sexes. This is explained by the fact that females always inherit an X chromosome from both father and mother while males always get their X chromosome from their mothers. We speak of this

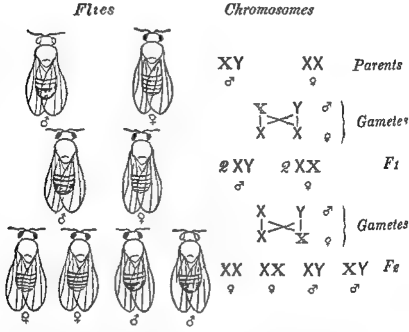


Fig 69—Sex linked inheritance of white and red eyes in *Drosophila*. Parents white eyed male and red eyed female. F red-eyed males and females. F red eyed females and equal numbers of red-eyed and white-eyed males. A black **X** indicates an X-chromosome bearing the gene for red eye; a white X bears white eye. **Y** is the Y-chromosome. (*From Conklin after Morgan*)

phenomenon as *crisscross inheritance*. There are many evidences that, in general daughters inherit more largely from fathers and sons from mothers and it is probable that the mechanism of this condition is like that just described. But to continue the reciprocal cross experiment to the F generation let us breed together the males and females of F. The result will be red eyed males and females in equal numbers (Fig 70)

The type of sex linkage which we have just described for *Dro*

sophila and which also prevails in man has come to be called the *Drosophila type* of sex linkage. There is however quite a different type that is called the *poultry type*, which while strikingly like the type already described differs from it in one important respect.

The poultry type of sex linkage.—In the *Drosophila type* the female is the homozygous sex (producing only one kind of gamete each

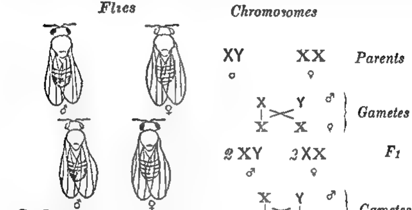


FIG. 70.—Reciprocal cross to that shown in Figure 69. Parents red-eyed male and white-eyed female. F_1 white eyed males and red eyed females ("criss cross inheritance"—Morgan). F_2 equal numbers of red eyed and white eyed individuals of both sexes. The distribution of the sex chromosomes is shown at the right as in Figure 69. (*From Conklin after Morgan.*)

with an X-chromosome) and the male is heterozygous (producing two kinds of gametes, one with an X and one with a Y chromosome). Now certainly in moths and butterflies and probably in birds the male is homozygous and the female heterozygous. It is the custom to designate the sex chromosome condition as WW for the male and WZ for the female, though why we should not use XX and XY it is difficult to say. With this reversal of sex chromosome composition of the two sexes we might expect that sex linked heredity would work out just

the reverse of that described for *Drosophila* so far as the sexes are concerned, and this interestingly enough, is exactly what we get

A typical instance of sex linkage of this sort is seen when a barred Plymouth Rock cock is mated with a Black Lanshan hen (Fig 71) All offspring both males and females of the F_1 generation are barred

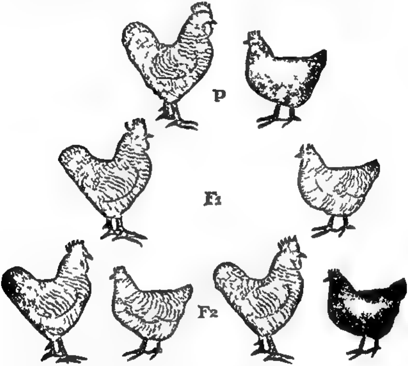


Fig 71 —Sex linked inheritance of barred and unbarred (black) plumage in poultry P parents barred male unbarred female F_1 barred males and females F_2 males all barred females in equal numbers barred and unbarred (*After Morgan*)

but when the individuals of F_1 are interbred (or the F_1 males are bred with any barred females) all males are barred and half of the females are barred and half are black Here we see that the recessive character black is linked with the *female* sex If we cross a black female with an F_1 male we can get equal numbers of barred and of black males and females The *reciprocal cross* (Fig 72) illustrates *crisscross* inheritance Starting with a black male and a barred female we get in F_1 barred males and black females When the F_1 individuals are interbred we get half barred and half black males and females

While in the birds the chromosomal condition has never been completely worked out on account of inherent technical difficulties likely to be overcome any day, the case of the currant moth *Abraxas* has been thoroughly analyzed. The sex linkage follows the poultry plan and the gametes of the male have been found to be all alike, while

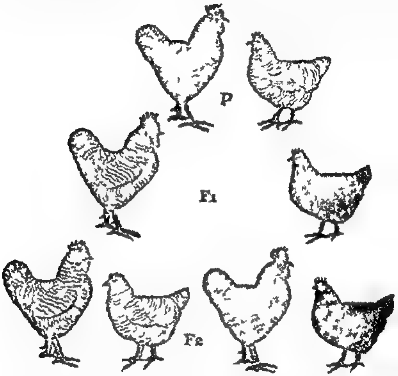


Fig. 72.—Reciprocal cross to that shown in Figure 71. P, parents unbarred male, barred female; F1, barred males, unbarred females (crisscross inheritance); F2, barred and unbarred birds equally numerous in both sexes. (*From Castle.*)

those of the female are of two types, one containing an X-chromosome (W-chromosome) and the other a Y-chromosome (Z-chromosome). The striking parallelism between the reversal in sex linked heredity and in the visible reversal of chromosome composition in these two groups of animals (*Drosophila* and man on the one hand, and the butterflies, moths, and birds on the other) offers one of the most cogent proofs of the validity of the chromosome theory of heredity which we have already come to rely upon and shall have further occasion to make use of later on.

To bring the facts of sex linked heredity sharply into focus by way of summary let us quote from D F Jones a genetic formulation of the whole matter

Rules for sex linked inheritance —From this series of facts the following rules governing the transmission of sex linked characters can be deduced

"1 When the *homozygous* sex transmits the *dominant* factor all of the offspring in the first generation exhibit the dominant character and the second generation is composed of three dominants to one recessive the latter having the same sex as the recessive grandparent

2 When the *homozygous* sex transmits the *recessive* factor, both dominant and recessive characters are exhibited in the first generation but exclusively upon the opposite sexes, and in the second generation both sexes show the sex linked characters in equal numbers"

CHAPTER XXIII

LINKAGE, CROSSING-OVER AND THE ARCHITECTURE OF THE GERM PLASM

Owing to the fact that most of the important advances in our knowledge of the finer structure of the heredity machine have been made with the aid of the little fly *Drosophila melanogaster* this chapter might be dedicated to the memory of this insect Although like Cinderella *Drosophila* comes from the humble environment of the garbage can says Walter yet this fly has easily outstripped all its sister competitors for genetical honors until today it stands probably as the most famous experimental organism in the whole world

But too much credit for the genetic revelations derived from a study of *Drosophila* must not be given to the fly which of its own accord would never have told us anything Though the name of *Drosophila* may now be famous all over the world the one who made it famous is *Professor T H Morgan* who in collaboration with an unusually able corps of assistants (especially Sturtevant Bridges and Muller) has demonstrated to the scientific world the value of co-operation in research The old adage that two minds are better than one has proven true in this long and arduous and above all fruitful investigation The work done by the fly squad as it has been affectionately called by fellow biologists has resulted in an analysis of the heredity machine so detailed as to be almost unbelievable It seems too good to be true yet the keenest critics of the work have failed to find any real flaws in the intricate fabric of conceptions that has been woven The whole story of this brilliant discovery or series of discoveries cannot be told in a way that would be intelligible to the layman or even to one with only a superficial knowledge of genetics . It requires long and arduous study to understand it all and one of the reasons why the ideas have failed of general acceptance is that only relatively few biologists have been willing to devote to the study of the data the amount of time and labor necessary fully to understand them

LINKAGE

In the last chapter a detailed account was given of the sex linked inheritance of white eyes in *Drosophila* This was the first of the sex

linked characters discovered in *Drosophila* but by no means the last Soon after the discovery of the white eye mutant there appeared in typical stock characterized by gray wing color a single male mutant distinguished by yellow wing color, and this character was found to be inherited exactly after the manner of white eyes In other words it is sex linked and therefore must have its gene in the X chromosome As time went on many new sex linked characters appeared as mutants always noted in males and these characters had to do with all sorts of bodily characters Several of these were new eye colors (vermilion ruby prune garnet) others had to do with eye shape or eye texture (furrowed, bar eye and small eye) others with wing size and shape (broad wing club wing cut wing vestigial wing) others with bristles (scute singed forked) others with body color (tan sable) and some were lethal characters Altogether over sixty definite sex linked mutant genes with their allelomorphs have been found to be sex linked and therefore must have their loci in the X chromosome

Now during the twenty years of breeding millions and millions of *drosophilas* and examining them for signs of new hereditary characters some hundreds of other mutations were noted and their modes of heredity studied This latter great collection of mutant characters showed no sex linkage so could not be assigned to the X chromosome They must in all probability be located in the *autosomes*, as the rest of the chromosomes are called But which of the remaining chromosomes carry the various non sex linked genes is not definitely known An important fact however soon came to light namely that practically all of these non sex linked genes fall naturally into two groups of nearly equal size The basis for this distribution of genes into two groups is this that some of the characters appear together more often than not while other characters appear apart (i e in separate individuals) more often than together in the same individual This process of classifying characters results in two large groups of characters of nearly equal size each rather more numerous than the sex linked group The two large classes of genes that seem to hang together in heredity more often than they go apart have come to be assigned to chromosomes II and III (Fig 53) respectively, and are known as the *second and third linkage group* At present it is not possible to distinguish between Chromosome II and Chromosome III, for they are of the same size and shape but the point is that there are only two other pairs of large chromosomes in *Drosophila* and only two large linkage groups besides the sex linked group What more natural

then than to assign these two large linkage groups to the two large chromosomes that are present?

All went well with the linkage hypothesis for awhile but before long one of the workers discovered a new character that was not at all linked with any of the three groups and therefore could not be assigned to any chromosome known at that time. This seemed at first like a staggering blow to the hypothesis then entertained but it turned out to be one of the best demonstrations of its validity. A re examination was made of the germ cells of *Drosophila* with the result that a pair of tiny chromosomes was found to be always present which because of their very small size had been overlooked by the original students of this material. This tiny chromosome was called Chromosome IV, and the new mutant bent wing was assigned to it. Some time later another aberrant mutant eyeless was found that was closely linked with bent and therefore assigned to Chromosome IV. So far these are the only genes that have been located in the tiny chromosome. This may mean that there is not room for many genes in so small a body.

Now if there is anything in the chromosome theory of heredity and if the genes of individual differences have their seat in the chromosomes all of the character differences in *Drosophila melanogaster* no matter how many are found must be in no more than four groups for there are only four kinds of chromosomes in that species. For a while it was feared that some new character would appear that was not linked with any of the known linkage groups for the discovery of such a character would strike a severe blow against the theory of link age and against the chromosome theory in general. After the passage of several years however and the discovery of almost a hundred new mutants *not one has been found that does not show linkage with one of the four known groups*. Just to the extent that the finding of a fifth group of characters would have weakened the chromosome theory to that extent the failure to find any exceptions to the four linkage groups strengthens the theory.

The characters represented by genes in both second and third chromosomes have to do with all parts of the body including eye color eye shape body color wing size and shape bristle characters leg form and lethal characters. It cannot then be said that any one chromosome carries genes characteristic of any one part of the body instead it seems that every chromosome carries genes that affect every part of the body or in other words the whole organism.

Confirmatory evidence of the validity of the theory of linkage comes from the comparative study of other species of *Drosophila*, some of which have the same number of chromosomes as has *D melanogaster*, others of which have a larger number In one species that has four pairs of chromosomes like the original species only four linkage groups have been found while in other species in which an extra pair of chromosomes has been found there is a fifth linkage group Comparative studies upon the linkage groups and the kinds of genes in these linkage groups have revealed a striking parallelism between the different species and a beautiful conformity between the numbers of chromosomes and the number of linkage groups Also it should be said that the relative numbers of genes discovered is in a rather definite proportion to the size of the chromosomes

CROSSING-OVER

All of our studies of the mechanism of heredity up till now have led to the conclusion that chromosomes are very definite and individual structures that continue from generation to generation intact and are passed as wholes from parent to offspring We have spoken of the process of pairing of homologous chromosomes in synapsis as though this pairing were no more intimate than a mere temporary embrace We have spoken as if during the reduction division to form gametes the homologous chromosomes merely part company and proceed intact to opposite poles of the dividing cell and enter separate gametes unaffected by having associated in the embrace of synapsis That this is far from true has been revealed by an exact numerical study of the varying degrees of linkage in the characters whose genes are supposed to be located in a single member of a given chromosome pair On the basis that a chromosome is an inviolable body proceeding as a whole from generation to generation we should of course expect any two characters that were once represented by genes in the same chromosome to stay together perfectly i e, always to appear together in the same individual The fact that this result was not realized led to further advances in our understanding of the complex heredity machine Let us see just how linkage works out with certain genes in the X-chromosome Remember that each of the characters was located in the X-chromosome because each one by itself followed the mode of heredity of a sex linked character

The mode of linkage of two sex linked genes —The wing color called 'yellow and the eye color called white have already been

dealt with in the previous chapter and were seen to be sex linked Now let us assume that by the proper breeding experiment we have a yellow winged white eyed female (call her yellow white for short) Mate her with an ordinary normal male with gray wing and red eyes (call him gray red) All the daughters are gray red like the father (each having inherited an X chromosome from him), but the sons are yellow white like the mother (having inherited her X chromosome) The Y-chromosome does not affect the result at all The daughters in addition to receiving an X chromosome from the father receive another X chromosome from the mother so they have two different X chromosomes They are all phenotypically gray red because gray and red are dominant over yellow and white

Now it is easy to test the composition of these hybrid females by breeding them with double recessive (yellow white) males The result is as follows 49 5 per cent of offspring are yellow white 49 5 per cent are gray red, 0 5 per cent are yellow red, and 0 5 per cent are gray white Such a result as this could hardly be anticipated If there were no linkage but entirely independent assortment as would be the case were the two pairs of genes in different chromosomes we should expect the dihybrid ratio of nine gray reds three gray whites three yellow reds and one yellow white If on the other hand chromosomes retain their integrity when they separate after synapsis we would expect 50 per cent gray reds and 50 per cent yellow whites Why do we find the anomalous ratios that we do? Obviously the chromosomes that pair in synapsis do not always part company without being affected by the chromosomal embrace but instead they seem at least occasionally to undergo a mutual exchange of equivalent genes Thus in one case in a hundred the gray and yellow wing allelomorphic genes are traded without also trading the red and white-eye genes and in exactly the same number of cases the red and white genes are traded between chromosomes without the yellow and gray being traded along with them This mutual and perfectly equitable exchange of genes between homologous chromosomes is called *crossin over* and the percentage of crossing over between any two allelomorphs is the same each time the same breeding experiment is repeated under the same conditions In the case we have just described the crossing over percentage is very small only 1 per cent. Let us try another pair of sex linked genes

A female with white eyes and miniature wings is bred to a male with red eyes and long (or normal) wings The miniature-wing gene

has already been shown to be sex linked The result in F_1 is that all females are red long and all males are white miniature Inbreed the individuals of F_1 and we get in F_2 33 5 per cent white miniatures, 33 5 per cent red longs, 16 5 per cent white longs and 16 5 per cent red miniatures In other words the crossing over percentage is 33 If the crossing over percentage were to equal or exceed 50 per cent, it would mean that there is no linkage at all for if the two allelomorphic genes were in different pairs of chromosomes we should have even chances of two independent characters coming together or staying apart Thus we may say that in the first experiment the linkage (99 per cent) is very high and the crossover percentage is very low (1 per cent) while in the second experiment the linkage is relatively weak (67 per cent or only 17 per cent stronger than no linkage at all) and the crossover percentage is relatively high (33 per cent)

The mechanism of crossing over — If it be admitted," say Morgan, Sturtevant Muller and Bridges, in their volume *The Mechanism of Mendelian Heredity*, that Mendelian factors are carried by chromosomes it can not be denied that interchange between homologous chromosomes must occur for sex linked factors cross over from each other and yet are known to be in the same pair of chromosomes since they all follow the X chromosome in its distribution The evidence allows no other interpretation But why should crossing over take place so rarely between certain factors and so often between others? We can make use here of certain information in regard to the chromosomes that gives a very simple answer to the question In the early germ cells before the maturation period begins the chromosomes appear to be scattered in the nuclei and the homologous chromosomes in many cases show no tendency to lie together, although in some animals *e g*, in many flies the members of a pair are often found side by side In this early period the germ cells divide as do other cells and thereby increase in numbers But at the termination of this period, the homologous chromosomes unite in pairs There has been much controversy as to how this union takes place but in some cases at least the uniting chromosomes twist around each other as they come together This is illustrated to the left in Figure 73 As a consequence parts of one chromosome will come to lie now on one, now on the other side of the mate If when the twisted chromosomes separate the parts on the same side go to the same pole the end result will be that shown to the right of Figure 73 Each chromosome has interchanged a part with its mate This process has been called crossing-over It is

of course also possible that the twisted chromosomes do not break and reunite where they cross and if they do not then when they begin to separate they simply pull apart irrespective of the side on which they lie When this occurs each chromosome remains intact and no crossing over takes place

"The chance that such a process of crossing over will occur between any two given points on the chromosome should obviously be greater the greater the distance between those points If then the Mendelian factors lie along the chromosomes the amount of crossing over between any two of them will depend upon their distance apart Should two points lie near together a cross over will only rarely occur between them if they lie farther apart the chance of such a cross-over taking place at some point between them will be greater From this point of view the percentage of crossing over is an expression of the distance of the factors from each other

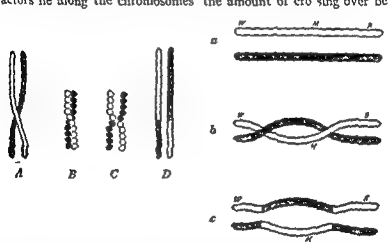


FIG 73—B and C illustrate Morgan's idea of the linear arrangement of the genes in the chromosomes A and D show how the composition of the chromosomes is supposed to change as the result of the cross over On the right a pair of chromosomes a before b during and c after a double crossover (*After Morgan*)

CHROMOSOMAL MAPS INDICATING THE ARRANGEMENT OF MENDELIAN FACTORS OR GENES IN THE CHROMOSOMES

By making use of the fertile idea explained in the last paragraph that the percentage of crossing over between any two factors indicates their relative distances apart it was possible to map out the rela

tive positions of all known factors The unit of distance on the map is that between two genes that have a crossover value of 1 per cent Haldane has proposed the term *morgan* for this unit of map distance These map units are only relative units not absolute as will be shown later The validity of the crossing over hypothesis and of the chromosome maps may be tested in an almost infinite number of ways For example let us take a simple case of the so called three point method of locating a new factor Suppose we have already determined the crossover percentage for two factors *A* and *B* to be 6 per cent A new factor C appears which belongs to the same linkage group as A and B and we wish to locate it First we work out its crossover percentage with *A* and it turns out to be 4 per cent We then can predict that the crossover percentage between *B* and *C* must be either 6+4 (10) or 6 −4 (2) If on working out the percentage it coincides with the theoretical prediction the method of locating genes in the chromosome receives strong support In practice it may be said the method works out perfectly for short sections of the map but breaks down somewhat for long map distances for the reasons indicated below

Double crossing over an explanation of apparent discrepancies between map distances and crossover percentages—This matter is best explained by the use of a concrete instance Let us take three sex linked genes white miniature and bar The crossover percentage observed between white and miniature as has already been shown is 33 that between miniature and bar is 22 The expected crossover percentage between white and bar is either 33+22 (55) or 33−22 (11) but the observed value is 44 per cent The proposed explanation of this apparently serious discrepancy is given by the authors of the theory as follows

"If we represent the percentages of crossing over as relative distances along the chromosome the three points will lie as shown in Figure 73 *a* If crossing over takes place between white and miniature and between miniature and bar then it might be expected sometimes to take place in both regions at once as shown in Figure 73 *b* The result here would be to produce two chromosomes like those shown in the lower figure (Fig 73 *c*) The combinations of factors which these two chromosomes resulting from double crossing-over would contain are white long bar and red miniature round Since these two classes of gametes are actually produced the results of the experiment fulfill the theoretical expectation

There is a corollary of importance to this conclusion When a cross is made that involves only white and bar, the double crossing over, that can be detected only when an intermediate point is followed must still be supposed to take place Whenever it does take place white bar flies and red round flies result These will be added to the non-crossover classes since they have the same external characteristics Consequently the non crossover classes will be increased and the crossover classes decreased In fact the sum of the two crossover percentages 33 and 22 (55) is much greater than the apparent amount (44) of crossing-over when only bar and white are involved Here then we have an explanation of why long distances taken as a whole give too little crossing over, as compared with the same distances taken section by section The lowered percentage is an actual necessity owing to the occurrence of double crossing over

Interference —One of the neatest confirmations of the crossover hypothesis is one that was first advanced by Muller According to this idea whenever double crossing over occurs two points of crossing over cannot be near together unless the chromosomes coil rather tightly about each other Consequently, if crossing over occurs at a given point there cannot be further crossing over at the same time at nearby points Now it has been actually demonstrated that this is true for genes in the neighborhood of a crossed over gene do not themselves cross-over with that gene in the degree expected on the basis of the law of probability This is supposed to be a sort of *interference* with free crossing over It may be supposed says Castle that chromosomes are somewhat like sticks of candy Break one in two at one point and it is unlikely that a break will occur simultaneously within a short distance of the first break the strain there being already relieved The fact that what must be expected in this case is actually realized in every case goes far toward establishing the validity of the whole crossing over hypothesis and the use of this hypothesis in showing the linear arrangement of the genes in the chromosomes

In this chapter it is hardly feasible to present any further evidence in support of the claims of the *Drosophila* school of geneticists that they have actually discovered the inmost secrets about the finer details of the mechanism of Mendelian heredity Suffice it to say that the evidence is voluminous and consistent. Not a single fact has come to light which is incompatible with the hypothesis and new facts are continually coming to light that agree with the hypothesis and lend it

further support The opponents of the hypothesis are yearly becom ing fewer and fewer, and the few remaining irreconcilables are having less and less to say It should be said, then in all fairness that the hypotheses discussed in this chapter have been most fruitful in leading to new discoveries and in last analysis this is the only fair test of a hypothesis If it is fruitful it is good

The crowning feat of the *Drosophila* workers is the making of the chromosome maps of the species studied While it is impossible to obtain the latest version of the map for the reason that new loci are continually being added the accompanying map (Fig 74) gives the locations of the genes that have been determined most carefully It will be noted that not only have the genes in the X chromosome been located but also those in the other three chromosome pairs A few additional situations that have arisen out of the studies involved in making the map will now be discussed and then this somewhat diffi cult chapter will be brought to a close

Multiple allelomorphs —In a previous connection we have dis cussed the multiple factor hypothesis as an explanation of quantita tive heredity Multiple factors are duplicate factors located in differ ent chromosomes Quite definitely in contrast with that situation is one in which different factors or different forms of the same factors occupy the same locus of the same chromosome For example red eye in *Drosophila* is a single factor A change in the red-eye factor gives white eye another change in red gives cherry, another gives eosin and several other definite mutant colors resulting from changes in red have been observed Now each of these changed color factors is an allelomorph of red and each is also an allelomorph of any of the others By this we mean that if a cross is made between individuals differing with respect to any two of these alternative colors of eye, one will be dominant over the other in the F generation and there will be three dominants to one recessive in the F generation One of the assumptions about allelomorphic genes is that they occupy equivalent locations in homologous chromosomes This can be put to a crucial test No more than two members of a set of multiple allelomorphs can be present in one individual because there are only two homologous chromosomes and hence only two equivalent gene loci This proves to be true for when red eye and white eye enter into a cross only these two eye colors come out of it when cherry and white go in only cherry and white come out when red and cherry go in only red and cherry come out Several other authors have found interesting sets of multi

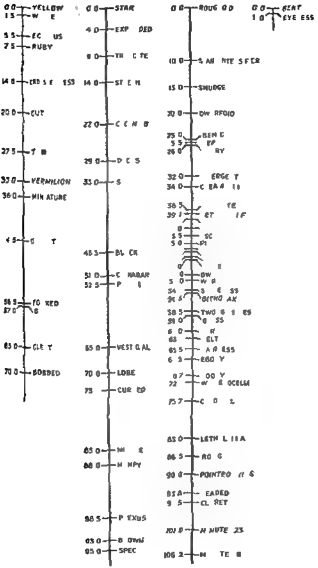


Fig 74 —The chromosome map of *Drosophila melanogaster* (*After Morgan and Bridges*)

ple allelomorphs in other animals Nabours, for example has described a very interesting series of these for the grasshopper *Hesperotettix* Sewall Wright has described a considerable number of such cases in guinea pigs and Bellamy has worked out an explanation of a very intricate piece of hereditary behavior in fish hybrids that involve the use of the multiple allelomorph scheme

Lethal factors again —A study of the chromosome map of *Drosophila melanogaster* will show that many of the located factors are *lethal* This perhaps needs further explanation Many of the factors that we have previously dealt with in this insect are more or less unimportant to the life of the animal Such things as slight changes in eye color body color, bristle arrangement etc are not very important, nor do they affect the viability of their possessors Some factors on the contrary, have been found to be so essential to the life of the individual that their absence causes death The loss of or detrimental change in a vital character is known as a lethal factor Of course all such factors are recessive otherwise they never could be inherited As it is, an individual may have a lethal factor in the heterozygous condition, balanced by the normal dominant character When however two such heterozygous individuals breed together one fourth of their offspring according to the simple Mendelian rule, will get the lethal factor from both parents These homozygous recessive lethal zygotes cannot live so the ratio that actually appears is one homozygous normal to two heterozygous individuals (phenotypically normal) and that is all One of the best known cases of this kind of hereditary behavior occurs in mice Yellow mice when mated together give one gray to two yellows The production of grays from yellows shows that the yellows were heterozygous or hybrid yellow and gray It is noted that the litters of these mice average one fourth smaller than other mice What becomes of the lost one fourth? An examination of the uteri of yellow mice reveals a number of dead embryos equal to the expected ratio of pure dominant yellows These constitute the missing class and prove the presence in yellow mice of the recessive lethal factor associated with the yellow factor

LINKAGE IN OTHER ORGANISMS

Lest the reader leave this chapter with the impression that linkage is a phenomenon confined to flies and mice we shall close this chapter with the table on the next page taken from Castle, which shows how widespread is the occurrence of linkage and crossing-over in both the

CASES OF LINKAGE IN PLANTS OR IN ANIMALS OTHER THAN DROSOPHILA

Species	[illegible]	Linked Characters	Cross-over Percentage	Linkage Strength	Authority
Sweet pea	1	Purple flowers, long pollen	11 or 12	76–78	Bateson and Punnett
	1	Purple flowers, erect standard	0.78	98.4	
	1	Long pollen, erect standard	12.5	75	
	2	Dark axil, fertile anthers	6.2	87.6	
	2	Dark axil, normal (not cretin) flower	?		
	2	Fertile anthers, normal (not cretin) flowers	25.0	50	
Primula sinensis	1	Short style, magenta corolla	34.[illegible]	32	Altenburg
	1	*Short style, green stigma*	40.6	18.8	
	1	Magenta corolla, green stigma	11.6	76.8	
	1	Tinged corolla, green stigma	?		Gregory
	1	Pale stem, green stigma	?		
Garden pea	1	Round seeds, tendrils on leaves	1.5	97	Bateson and Vilmorin
	2	Late flowering, colored flowers	12–16	68–76	Hoshino
Antirrhinum	1	Red flower color, picturatum pattern	20.[illegible]	60	Baur
Maize	1	Waxy endosperm, Aleurone C	26.7	46.6	Breggar
	2	Aleurone R, Chlorophyl G	19.0	62?	Lindstrom
	2	Aleurone [illegible], Chlorophyl L	0.0	100	
	2	Chlorophyl G, Chlorophyl L	23.0	54	
	3	Starchy endosperm, tunicate seed	8.3	83.4	Jones
Tomato	1	Vine habit, fruit shape	20.0	60	Jones
	2	Green foliage, 2 celled fruit	0?	100?	
Beans	1	Seed pattern, vine habit	0?	100?	Surface
Silkworm	1	Pattern Q of larva, yellow silk	26.1	47.8	Tanaka
Apotettix	1	Patterns G and M	4 (in ♀)	92	Nabours
	1	Patterns M and K	1 (in ♀)	98	
	1	Patterns K and Y	6 (in ♀)	[illegible]	
	1	Patterns Y and R	10 (in ♀)	80	
	1	Patterns Y and T	12 (in ♀)	76	
	1	Patterns R and T	0 (in ♀)	100	
	1	Patterns M and R	10 (in ♀)	80	
	1	Patterns Y and Z	10 (in ♀)	80	
Pigeon	1	Sex linked factors I and A	40 (in ♂)	20	Cole and Kelley
Rat	1	Albinism, red-eye	1.0?	98?	Castle and Dunn
	1	Albinism, pink-eye	21.0	58	
	1	Red eye, pink eye	18.3	63.4	
Mouse	1	Albinism, pink-eye	14.3	71.4	Castle and Dunn

animal and the plant kingdom In all probability it is a universal phenomenon, and if so, takes place in man There are in fact, strong indications in man that fair hair and blue eyes are linked but they show also considerable crossing over Similarly, red hair and a certain type of disposition are popularly supposed to be linked but crossing over may be a saving grace in this as in other cases

With this chapter we have arrived at the climax of discovery in the field of the mechanism of heredity This is undoubtedly the most intricate consideration dealt with in this volume In its very nature it is relatively difficult to understand We have tried to explain everything in a decidedly circumstantial way and it is hoped that some success in an endeavor to attain clearness has been attained

CHAPTER XXIV

CROSS BREEDING AND INBREEDING

Cross breeding is essentially the same as hybridization and we have already studied various phases of hybridization in connection with Mendelian heredity There are however certain other aspects of cross breeding that have only a more or less remote connection with Mendelian analysis

The rôle of hybridization in evolution —"This says R R Gates is a thorny subject on which different investigators have taken quite different attitudes to the same facts The extreme view that all flowering plants or even all sexual organisms are hybrids has been held This has been accompanied in some cases (Lotsy) by the denial of any true germinal change though why such labile substance as protoplasm should be incapable of undergoing a permanent or germinal change is difficult to understand Jeffries and others appear to hold that polyploidy and other changes in which hybridization may be a factor have nothing to do with evolution A more reasonable view would appear to be that crossing has occurred in various groups from time to time with more or less frequency and between sometimes more and sometimes less closely related forms Crossing is therefore a condition under which much evolution has taken place It by no means follows that crossing any more than gravitation is a *vera causa* still less *the vera causa* of evolution, but it is a contributing condition Polyploidy frequently accompanied by hybridization appears to be a common occurrence among flowering plants but it would be futile to deny on this account that flowering plants have had an evolution nor would it be safe to assume at present that the evolution of this group differs very essentially from that of any other

The exact rôle of hybridization in the formation of new species is at present merely a matter for speculation but that many new races have been the result of favorable combinations of the genetic factors of different strains can scarcely be doubted In a sense it may be said that hybridization is the rule in all organisms that reproduce sexually for no completely homozygous individuals exist in such groups and therefore there will always be a certain amount of factor segregation in gamete formation and of recombination in the process of zygote formation Also it must be admitted that there are all grades of hetero

zygosity within a species and between one species and another. Moreover, sexual reproduction as an adaptation operates chiefly through bringing together a variety of combinations of characters possessed by strains genetically diverse, it is, in fact a hybridizing mechanism. It seems probable therefore that hybridization as a factor in evolution operates up to the limit of the adaptive possibilities inherent in its mechanism. We may therefore conclude that hybridization is and has been an important evolutionary factor, though we have at present little information as to its precise mode of operation as an agent in species formation.

SOME ANIMAL HYBRIDS

One of the arguments offered by the advocates of the theory that hybridization has played a prominent part in species forming in nature is that man has carried on so much successful hybridization between different species of animals and plants and has produced many very useful hybrids some of them better adapted than either of the parent types from which the hybrids were derived.

Especially interesting are animal hybrids produced by interbreeding distinct species of domestic and wild animals. Our brief account will be confined to horse, cattle, and fowl hybrids.

Horse hybrids.—These hybrids are all the product of crossing different species of the genus *Equus*. The commonest hybrid is that between the mare of the horse proper *Equus caballus* and the jack of the species *E. hemionus*. The result is the mule, a useful domestic animal combining some of the best features of the two species and superior to either in vigor, hardiness, capacity for work and resistance to disease. The reciprocal cross, made by mating a jennet to a stallion, is called a "hinny," a sort of small mule. Neither mules nor hinnies are, as a rule, fertile so they are not self perpetuating. The rare reports of female mules giving birth to foals when bred to jacks are as yet not fully authenticated. There is some possibility that the particular females in question were either rather large jennets, which of course would be fertile or rather mulelike mares.

The sterility of mules has been shown by Wodsedalek to be due to differences in the numbers of chromosomes in the two species, the horse having in the female 18 autosomes and 2 X chromosomes, the male 18 autosomes and one X-chromosome; the ass having in the female 32 autosomes and 2 X chromosomes, the male 32 autosomes and (according to Paynter) an X and a Y-chromosome. With this great discrepancy in chromosomes it is hardly to be expected that meiosis could operate so as to give any sort of viable gametes or zygotes.

A number of other *Equus* hybrids have been produced The horse has been crossed with the now extinct quagga (*E quagga*) and with several species of zebras And the zebras have been crossed with asses · No particular use has been made of such hybrids

Cattle hybrids —There are many species of the genus *Bos* The auroch is designated *Bos taurus primegenus* The now extinct wild ox of Europe supposed to be the ancestor of European cattle is called *Bos taurus* The characteristic humped cattle of India is known as *Bos indicus* The wild ox of Java is called *Bibos sondaicus* and hence belongs to a different genus The bison of Europe and the closely related American bison are called, respectively *Bison bonasus* and *Bison bison* There are three species of buffalos belonging to the genus *Bubalus* Various hybrids both interspecific and intergeneric have been made by crossing these and other species of cattle like animals Hybridization of European and Brahman cattle or zebus (*Bos indicus*) has been carried on very successfully in the southern states especially in Texas and Louisiana The hybrids are vigorous and both sexes are fertile The F_1 hybrids are predominantly of the European breed with only the suggestion of the zebu hump and much less of the hang ing dewlap than in pure zebus When the F individuals are interbred there is a great deal of variation among the F offspring of which no satisfactory analysis has yet been made The chief advantage de rived from introducing the zebu strain into American cattle is that zebus are immune to Texas fever and hybrids with as low as one eighth zebu blood are also immune to this most serious of cattle diseases

Bisons and European cattle have been successfully crossed, the cross usually made being between cattle cows and bison bulls The cross is successful only in a small percentage of cases and very fre quently both dam and calf are lost The sex ratio of these hybrids is very unequal the ratio being at one time 33 females to 6 males Usually the F_1 males are sterile but the females are fertile and may be back-crossed to bison bulls or cattle bulls as desired and there is no difficulty or danger of loss of life as in the F_1 cross Animals that are the product of various grades of admixture of bison and cattle are called *cattalos* It is expected that by selection a desirable hybrid type may be fixed, combining the best features of both genera

Fowl hybrids —The domestic fowl is commonly designated *Gallus domesticus* and is believed to have been derived from one or more of several wild species of the genus *Gallus* Four wild species are recog nized *G gallus* the red jungle fowl of northern India Malay states

and Sumatra, *G lafayette* the Ceylon jungle fowl *G sonnerate* the gray jungle fowl of southern India and *G varius* the jungle fowl of Java These birds are rather wild and do not hybridize well in captivity Yet occasional uncontrolled hybrids have been produced which are of interest in throwing some light on the origin of the various domestic breeds Darwin was of the opinion that all the domestic breeds have been derived from *G gallus*, for sometimes in India cocks of *G gallus* invade flocks of domestic fowls and mate with the hens producing fully fertile offspring The same has been claimed since Darwin wrote for the other species and some authors are inclined to believe that domestic fowls of different breeds may have been derived from different wild species of *Gallus* The evidence for the latter view however is less abundant than for Darwin s contention

SECONDARY EFFECTS OF CROSS BREEDING AND INBREEDING

A. CROSS BREEDING

Hybrid vigor (heterosis)—It has long been known that the crossing of different races varieties or even species of animals or plants result in the production of first generation hybrids characterized by a greater sturdiness vitality, and size than either parent species This effect has received the name *hybrid vigor* or *heterosis* A good example of this effect is the common mule, which is large and strong thrives under adverse conditions, and is hardier than either parent It has the disadvantage or possibly advantage of being sterile a fact which makes it necessary to hybridize two species every time we want another mule.

Some of the manifestations of hybrid vigor as observed in various crosses are as follows

a) Hastening of maturity—This is particularly advantageous in plants reared in regions where the growing period is short Thus hybrid strains of cereals may be valuable because they can be harvested sooner than pure bred strains It is also true that hybrid plants such for example as tomatoes have a larger as well as an earlier yield.

b) Increased longevity—Pearl has shown that hybrid strains of fruit flies have a longer average life-span than pure races The same is true for a number of hybrid races of plants as brought out by Gaertner

c) Better viability—The writer has shown that the hybrids produced by crossing the eggs of the fish *Fundulus heteroclitus* with the sperm of *F majalis* were frequently more viable faster growing, and more vigorous than the pure-bred young of either species but the hybrids from the reciprocal cross showed much reduced viability

Similarly he has shown that some of the hybrids produced by crossing the eggs of the sea urchin *Strongylocentrotus purpuratus* with the sperm of *S franciscanus* lived nearly twice as long under cultural conditions as did either pure breed while the reciprocal cross showed very low viability

d) Augmented facility of vegetative propagation —Many hybrid plants are noted for their success in vegetative propagation It is believed that plants such as strawberries brambles grasses etc that propagate so successfully by vegetative methods are the products of hybridization The vegetative method of reproduction not only maintains a fortunate combination of genetic characters that could hardly be repeated by gametic reproduction but maintains their hybrid vigor as well

These and perhaps some other effects all of which are essentially beneficial have been noted in both animals and plants The following explanation of hybrid vigor has been given by D F Jones

Explanation of hybrid vigor —From the illustrations given it is evident that there is a tendency for the features of both parents to be expressed in the offspring This is the basis for an understanding of the vigor derived from crossing There is a greater number of different hereditary factors in a hybrid individual than in either pure parent Nearly all variations that are recessive are less favorable to the development of the organism than their dominant mates Since crossing brings out those qualities which help the individual in its growth and suppresses the abnormal and unfavorable characters it is to be expected that hybrids will tend to be strong and vigorous This will be true however, only if each parent is able to supply the deficiency of the other and if the forms crossed are not so diverse that their union is incompatible with normal growth If the parents are themselves hybrids further crossing may bring together no great number of dominant favorable growth factors but may even uncover recessive characters Hence further crossing can not usually increase size and vigor and in fact may even result in the appearance of weaknesses This is clearly understandable from the operation of Mendel s principles of heredity

The question now arises as to whether hybridization in general is advantageous or the reverse Undoubtedly first generation hybrids are generally an improvement upon either parent race especially if the parents belong to races not too distantly related If we could stop hybridization after one generation, as Nature stops it in the case of the

mule nothing but good would apparently come out of it, but in man and among other animals and plants where mating is more or less indiscriminate cross breeding is sure to continue into the F F, and subsequent generations, entailing the production of all sorts of unfortunate combinations and the outcropping of all sorts of unbalanced recessive weaknesses In view of these considerations it is practically certain that hybridization unless accompanied by rigid selection and the elimination from parentage of the less desirable combinations, is on the whole disadvantageous In nature natural selection serves to eliminate sooner or later the worst combinations resulting from continuous cross-breeding but in man little is done to prevent the worst racial admixtures from predominating the result being that the populations of some parts of the New World are made up mainly of a rather homogeneous hybrid type possessing little more than the worst traits of the various races that have contributed to the melting pot

By way of a general summary let us quote the following paragraphs from D F Jones by whose book *Genetics in Plant and Animal Improvement* this discussion has been largely suggested

"*Summary*—From the foregoing it will be realized that if any individual is deficient or handicapped in its hereditary make up there is a good chance that its needs will be supplied when it is crossed with other individuals because all are not apt to be wanting in the same things What one lacks is furnished by the other and conversely, In other words there is a pooling of hereditary resources with the result that the combined effect is better than either could produce alone

"It should now be clear that the beneficial effects of crossing follow from the workings of the laws of heredity and not from any mysterious stimulus from the act of crossing itself If good qualities exist in the parents, but not in sufficient amount or not in their proper association, then there is a good opportunity for the offspring to bring together the favorable factors from both and surpass their parents in development This is a temporary and transitory effect however The increased vigor is shown at its best only in the first generation following the cross and is quickly lost in later generations unless it can be perpetuated by some form of asexual reproduction "[1]

B. INBREEDING

There is a widespread and deep-seated feeling among men that the mating of close relatives is unnatural and harmful In most civilized countries there are laws both religious and civic forbidding the mar

[1] *Loc cit*

riage of close relatives The aversion to the marriage of relatives has sometimes gone beyond the limits of genetic relationship and has invaded the realm of merely legal or conventional relationships as in England where it is or at least once was illegal to marry one s deceased wife s sister

Only exceptionally, as in the case of the royal families of Egypt and ancient Peru says Castle "has the marriage of brother and sister been sanctioned The underlying reason in such cases was the belief that the family in question constituted a superior race whose members could find no fit mates outside their own number There was probably no thought that inbreeding itself was beneficial but only the desire to conserve the superior excellence believed to reside in certain individuals The same considerations probably have led to the occasional practice of inbreeding in animal husbandry, viz , the desire to conserve and perpetuate the superiority of particular individuals

It appears that Robert Bakewell a stock breeder of the eighteenth century was the first to show the value of close inbreeding in maintaining a uniform type of sheep and cattle Bakewell adopted the plan of mating brother with sister or parent with offspring much to the horror of his neighbors who considered such a procedure immoral but their scruples were soon broken down by the obvious improvements obtained and the greatly increased revenue that accrued The practice of inbreeding has been a favorite one for a long time, and many fine breeds of standard character have been produced mainly in this way

Opinions among breeders differ as to whether inbreeding if practiced expertly is injurious Some believe that inbreeding itself involves no possible injury others hold that it is always more or less harmful In order to settle this question geneticists have carried out extensive experiments under conditions of rigid control Even these do not agree in their results One group of workers (Crampe and Ritzema Bos) found after extensive inbreeding of rats that there was a steady falling off in fertility and general health during the first six generations of inbreeding The material used however was a mixed or hybrid stock to start with a fact that makes a satisfactory conclusion difficult. Weismann inbred a race of white mice for twenty nine generations In the first ten generations the average number of young was 6 1 in the second ten generations it was 5 6 and in the last nine generations it was 4 2 Again nothing was known about the genetic constitution of the original parents

Recent experiments carried out by Dr Helen Dean King at the

Wistar Institute are entirely contrary to those of the workers just mentioned This piece of work was carried out in a most precise manner with large numbers of individuals The original stock consisted of four rather undersized but otherwise normal albino Norway rats Brothers and sisters were mated throughout the experiment For six generations no selective mating was practiced, with the result that many of the defects previously noted were in evidence but after the sixth generation some twenty females from about a thousand were selected for their superior qualities From this stock the result of inbreeding for twenty five generations was very good Dr King seems to have produced an essentially homozygous race of white rats that are superior in many ways to the race from which they have been derived. It seems probable that selection has rid the race of all or nearly all of the residual recessive characters so that the present combination is highly normal and standard Sewall Wright under the auspices of the United States Department of Agriculture, has carried out a very extensive program of inbreeding with guinea pigs His results are more in harmony with those of earlier workers than with those of Dr King In general the result of brother and sister mating was a steady loss of vigor both bodily and reproductive Both prenatal and postnatal mortality was increased Some families however remained quite strong after long inbreeding while other families declined so rapidly that it was impossible to perpetuate them after a few generations Some strange combinations of traits appeared in different stocks One stock was characterized by very low vitality, but remained normal in body size and in number of young produced Another stock showed undiminished vitality but greatly lowered reproductivity and reduced size The chief difference in method used in these two modern experiments seems to be that only the best were bred in Dr King s experiments while in Dr Wright s experiments no such precautions were taken probably because he preferred to approximate natural conditions

A large amount of experimentation in inbreeding has been carried out with domestic animals and plants of all sorts, and the results have shown as much diversity as those already reported consequently opinions are still at variance as to the question whether inbreeding is injurious per se D F Jones who seems to have given this matter very careful consideration takes the position that *"the only injury that comes from inbreeding comes from the inheritance received"* If the individuals inbred possess many undesirable recessive characters nothing

is surer than that inbreeding will bring these to the surface Cross breeding might succeed in masking such recessive characters but they remain in the germ plasm nevertheless All inbreeding does is to reveal that which was masked behind dominant characters Therefore it is not inbreeding itself that is to blame but a poor heredity In breeding is a valuable instrument for detecting the unfavorable hereditary characters in a race and giving the breeder a chance to cull out the defective factors from his stock

Inbreeding should be followed by cross breeding inbred stocks — Whatever loss of vigor or productiveness may be incidental to the in breeding method of standardizing stock may be entirely done away with by suitable cross breeding or outbreeding No matter how good an inbred stock may be great improvement can be brought about by introducing new blood even from an apparently very similar strain which is unrelated It is well known that when two pure breeds are crossed there is an effect quite equivalent to that which we have called hybrid vigor The animal breeder commonly practices close inbreeding in building up families of superior excellence which he maintains as pure-line stock used for crossing with other stocks in order to produce exceptional F_1 offspring Man of course cannot practice this scheme in the present state of society but it seems obvious that there lie in this method almost untold possibilities for racial improvement

CHAPTER XXV

CHANGE FACTORS INTRODUCTION

Change has already been contrasted with diversity by citing the analogy of the kaleidoscope (p 187) Another analogy may help to emphasize this difference If one were to shuffle and deal a very elaborate deck of cards the hands dealt would show very great diversity, but there would be a certain statistical limitation to the number of possible combinations of cards After a time the whole series of possible combinations would be dealt out and the series would go on repeating itself and nothing new would appear so long as the cards remained unchanged Add a new card or a new series of cards, or merely change some of the spots on a card, and at once the whole character of the combinations produced would be altered Dealing an unchanged deck of cards is the sort of thing that the diversity mechanism (sex) does but the mutation mechanism actually adds new cards or alters the spots Changes in the germinal substances themselves are called *mutations* Hence mutation is *the* change mechanism

CHANGING VIEWS AS TO THE ORIGIN OF NEW HEREDITARY CHARACTERS

Lamarck believed that all evolutionary change was initiated in the body (soma) directly or indirectly in response to environmental stimuli, causing increased or decreased functioning of parts He had no theory as to how such changes could be inherited but assumed that they were This belief is embodied in his theory of the inheritance of acquired characters, known as the "Lamarckian theory

Charles Darwin also believed that all variations that are frequent enough to serve as the raw material for selection originated in the soma in response to differences in the environment or indirectly, to changes in the amount of use to which a given part was put To account for such changes being hereditary he proposed a theory with which he was not very well satisfied for he called it ' the provisional theory of pangenesis ' According to this view, each part of the organism is continually giving off into the blood stream minute particles, ' pangenes each of which is characteristic of the particular status of a part of the organism at the time when the pangene was given off Thus a strengthened muscle or a more efficient eye, each resulting from in

creased functioning would give off pangenes reflecting muscle or eye improvements Similarly, a deteriorating organ or tissue or even a damaged or diseased part would produce pangenes reflecting their condition Now these pangenes were believed to be collected in the gonads to form germ cells a germ cell being a concentrated mass of all the kinds of pangenes of the organism In this simple way somatic changes were believed to be *inherited* *But the difficulty with this theory is* that no such mechanism exists

Weismann was the first biologist to depart from the idea that hereditary changes originate in the soma He proposed the theory of the continuity and apartness of the germ plasm and its corollary that all hereditary changes arise directly in the germ plasm His picture of the method of germinal change is expressed in his theory of germinal selection '

The essential feature of germinal selection as the name implies is a transfer of the struggle for existence to the germ cell The germ cell is assumed to be a greatly reduced and simplified sample of the characters of the whole organism Each independently variable part of the organism is supposed to be represented in the germ cell by a minute physiological unit, unique in composition and capable of reproducing the part in question in a new organism These hereditary units are called determinants ' Thus there is a different kind of determinant for each muscle of the body, for each bone or for each independently functioning blood vessel but since all red blood corpuscles are alike there would be only one determinant for all of them These determinants have to grow and in cell division to divide so as to furnish to daughter germ cells all of the necessary determinants for a whole individual In their process of growth and multiplication which goes on very rapidly at certain periods in the germ cell cycle these determinants are in competition among themselves for the available food supply Some may be more favorably placed than others or may be more active chemically than others There will thus arise a struggle within the germ for a chance to grow and reproduce their kind which for these determinants might be as bitter as would be the struggle in nature among the whole organisms that are in competition for a place in the world A determinant favored perhaps accidentally or possibly because of inherent activity by a good food supply would wax stronger and grow faster and would logically produce a larger and more effective part when that particular germ cell developed into an adult Other germ cells that would be the offspring

of this germ cell would continue the struggle among determinants, and it would be expected that the strong determinant would continue to gain further advantage until the structure it represents reached its maximum efficiency Similarly, a determinant that was for some reason deprived of its fair share of nutriment at any time would be weakened and would produce in cell division weakened daughter determinants These in turn unless especially favored would wage a losing fight and continue to grow smaller and weaker Each individual that might develop from such germ cells would have the characters whose determinant had been weakened in a reduced and progressively degenerating condition Finally certain determinants might starve entirely and the part for which they stood would disappear entirely from the ontogeny of the individual arising from these germ cells

In this way Weismann tried to explain the gradual dwindling and the final elimination of useless organs So also he would explain definitely directed or orthogenetic variations, because germinal selection, once started in a given direction, continues automatically till the goal of adaptiveness is reached

The most potent objections to the theory of germinal selection are as follows

1 There should be according to this theory, certain pronounced tendencies in variability in definite directions, whereas fluctuating variations nearly always distribute themselves evenly about the mean or mode and the same specific mean or mode is stationary in successive generations

2 The theory implies too rapid and too general modification of parts and therefore does not accord with the fact that species are decidedly constant except for occasional mutations over long periods of time To meet this objection Weismann proposes a new self correcting mechanism that checks too rapid a development of characters.

3 The over or undernourishment of determinants might conceivably induce size changes in characters already present but could hardly be responsible for the origin of qualitatively different characters

4 Actual experiments in over and underfeeding of animals have been carried on by certain experimenters in order to test out the theory of germinal selection In the experiments of Kellogg, for example involving feeding silkworm larvae only one eighth of the normal amount of food the only result was that the mature individuals were

dwarfed in size ; The relative sizes of the parts were unaltered show ing that there had been no real struggle among the determinants for on the theory of germinal selection only the stronger determinants would have survived and the weaker ones would have been starved out. Partial individuals moreover, lacking certain organs and over developed in others would have been produced instead of individuals merely smaller in all parts

These are the specific objections to the theory, but more important than all of these is the general objection that follows

Thus Weismann ' says Morgan, has piled up one hypothesis on another as though he could save the integrity of the theory of natural selection by adding new speculative matter to it The most unfortunate feature is that the new speculation is skilfully removed from the field of verification and invisible germs whose sole functions are those which Weismann s imagination bestows on them are brought forward as though they could supply the deficiencies of Darwin s theory This is indeed the old method of the philosophizers of nature An imaginary system has been invented which attempts to explain all difficulties and if it fails then new inventions are to be thought of Thus we see where the theory of selection of fluctuating germs has led one of the most widely known disciples of the Darwin ian theory

' The worst feature of the situation is not so much that Weismann has advanced new hypotheses unsupported by experimental evidence but that the speculation is of such a kind that it is from its very nature unverifiable and therefore useless Weismann is mistaken when he assumes that many zoologists object to his methods because they are largely speculative The real reason is that the speculation is so often of a kind that cannot be tested by observation and experiment.

It seems almost impossible that the same Professor Morgan who wrote the foregoing paragraphs in 1903 should now be the leading exponent of a theory of the mechanics of hereditary transmission which depends upon hereditary units almost identical with Weismann s determinants for the genes or factors of Morgan are minute corporeal bodies in the germ cells which determine the charac ters of the adult individual

The difference is however that the genes of Morgan are experi mentally demonstrable and have behind them a vast amount of real evidence for their existence

From T H Morgan *Evolution and Adaptation*

MUTATIONS

Mutations are by definition changes in the germinal substance. They may affect individual genes or whole bundles of genes (chromosomes). They may occur in the germ track or in the soma. If they occur in the soma the resulting change is seen in a local patch of changed cells the size of which depends on whether the mutation occurred early or late in ontogeny. Since body cells do not produce germ cells, somatic mutations are no more heritable than are functional changes in the soma. The only mutations of significance for evolution are those that occur in the germ track. The various kinds of germinal mutations will be discussed at some length in the following chapter.

CHAPTER XXVI

THE MUTATION THEORY

It will be recalled that Darwin although depending upon the ever present fluctuating variations as the material for natural selection *to work upon recognized the occasional occurrence of sports or* saltatory variations These however seemed to him to be so rare in nature as to offer no adequate basis for selection During the latter part of the nineteenth century several investigators feeling the inadequacy of fluctuating variations to produce qualitatively new characters decided to make a more careful examination of animals and plants in nature in order to discover whether saltatory variations might not be of more frequent occurrence than Darwin had supposed

In England William Bateson collected a large number of instances of a type of variation which he called *discontinuous* in contradistinction to the *continuous* type which we have been calling fluctuations Such variations instead of being in a closely graded series with the typical variations of a species were frequently quite sharply different from the majority Although no experiments were conducted in order to test the heredıtability of these discontinuous variations it is probable that some of them were mutations in the sense of De Vries

At about the same time Hugo De Vries in Holland partially as the result of his rediscovery of Mendel s work and his confirmation of the latter s laws of heredity, became convinced that new species arise not by the accumulation, through natural selection of minute fluctuating variations but by the sudden appearance in one generation of fully formed new elementary species He began a systematic research for species of plants in nature that were giving rise to new species Many species were examined in their natural surroundings and were then brought into the experimental garden for more careful observation but for a long time the search for a species throwing off new elementary species was unsuccessful Finally however, in a field near Hilversum in the vicinity of Amsterdam he found what seemed to him to be just the kind of plant he had been looking for in the evening primrose (*Oenothera lamarckiana*)

'Lamarck's evening primrose (Fig 75), says De Vries "is a stately plant with a stout stem attaining often a height of 1 6 meters and more When not crowded the main stem is surrounded by a large

FIG 75 —*Oenothera lamarckiana* the original type used by De Vries in his experiments This is the tock from Hilversum from which arose in successive generations a series of mutants (*From De Vries*)

circle of smaller branches growing upwards from its base so as to form a dense brush The flowers are large and bright yellow attracting immediate attention even from a distance They open toward evening, as the name indicates and are pollinated by bumble-bees and moths

On account of the classic character of De Vries s mutants of *Oenothera lamarckiana* we shall follow his own detailed description of the more significant of these

NEW SPECIES (MUTANTS) OF *OENOTHERA*[1]

HUGO DE VRIES

This striking species (*Oenothera lamarckiana*) was found in a locality near Hilversum in the vicinity of Amsterdam where it grew in some thousands of individuals Ordinarily biennial it produces rosettes in the first, and stems in the second year Both the stems and the rosettes were at once seen to be highly variable, and soon distinct varieties could be distinguished among them

The first di covery of this locality was made in 1886 Afterwards I visited it many times often weekly or even daily during the first few years and always at least once a year up to the present time This stately plant showed the long sought peculiarity of producing a number of new species every year Some of them were observed directly on the field, either as stems or as rosettes The latter could be transplanted into my garden for further observation and the stems yielded seeds to be sown under like control Others were too weak to live a sufficiently long time in the field They were discovered by sowing seed from indifferent plants of the wild locality in the garden A third and last method of getting still more new species from the original strain was the repetition of the sowing process by saving and sowing the seed which ripened on the introduced plants These various methods have led to the discovery of over a dozen new types never previously observed or described

Leaving the physiological side of the relations of these new forms for the next lecture it would be profitable to give a short description of the several novelties To this end they may be combined under five different heads according to their systematic value The first head includes those which are evidently to be considered as varieties

[1] From H De Vries *Species and Varieties* (copyright 1904) Used by special permission of the publishers The Open Court Publishing Company

in the narrower sense of the word, as previously given The second and third heads indicate the real progressive elementary species, first those which are as strong as the parent species, and secondly a group of weaker types, apparently not destined to be successful Under the fourth head I shall include some inconstant forms and under the last head those that are organically incomplete

Of varieties with a negative attribute or real retrograde varieties I have found three all of them in a flowering condition in the field I have given them the names of *laevifolia brevistylis* and *nannella*

The *laevifolia*, or smooth leaved variety was one of the very first deviating types found in the original field This was in the summer of 1887 seventeen years ago It formed a little group of plants growing at some distance from the main body in the same field I found some rosettes and some flowering stems and sowed some seed in the fall The variety has been quite constant in the field neither increasing in number of individual plants nor changing its place though now closely surrounded by other *lamarckianas* In my garden it has proved to be constant from seed never reverting to the original *lamarckiana* provided intercrossing was excluded

It is chiefly distinguished from Lamarck s evening primrose by its smooth leaves as the name indicates The leaves of the original form show numerous sinuosities in their blades not at the edge, but anywhere between the veins The blade shows numbers of convexities on either surface, the whole surface being undulated in this manner it lacks also the brightness of the ordinary evening primrose or *Oenothera biennis*

These undulations are lacking or at least very rare on the leaves of the new *laevifolia* Ordinarily they are wholly wanting, but at times single leaves with slight manifestations of this character may make their appearance They warn us that the capacity for such sinuosities is not wholly lost but only lies dormant in the new variety It is reduced to a latent state exactly as are the apparently lost characters of so many ordinary horticultural varieties

Lacking the undulations the *laevifolia*-leaves are smooth and bright They are a little narrower and more slender than those of the *lamarckiana* The convexities and concavities of leaves are a useful character in dry seasons but during wet summers such as those of the last few years they must be considered as very harmful as they retain some of the water which falls on the plants, prolonging the action of the water on the leaves This is considered by some writers

to be of some utility after slight showers but was ob erved to be a source of weakness during wet weather in my garden preventing the leaves from drying Whether the *laevifolia* would do better under such circumstances, I have however omitted to test

The flowers of the *laevifolia* are also in a slight degree different from those of *lamarckiana* The yellow color is paler and the petals are smoother Later in the fall on the weaker side branches these differences increase The *laevifolia* petals become smaller and are devoid of the emargination at the apex becoming ovate instead of obcordate This shape is often the most easily recognized and most striking mark of the variety In respect to the reproductive organs the fertility and abundance of good seed the *laevifolia* is by no means inferior or superior to the original species

O brevistylis, or the short styled evening primrose is the most curious of all my new forms It has very short styles which bring the stigmas only up to the throat of the calyx tube instead of upwards of the anthers The stigmas themselves are of another shape more flattened and not cylindrical The pollen falls from the anthers abundantly on them and germinates in the ordinary manner

The ovary which in *lamarckiana* and in all other new forms is wholly underneath the calyx tube is here only partially so This tube is inserted at some distances under its summit The insertion divides the ovary into two parts an upper and a lower one The upper part is much reduced in breadth and somewhat attenuated simulating a prolongation of the base of the style The lower part is also reduced but in another manner At the time of flowering it is like the ovary of *lamarckiana* neither smaller nor larger But it is only reached by very few pollen tubes and is therefore always very incompletely fertilized It does not fall off after the fading away of the flower as unfertilized ovaries usually do neither does it grow out nor assume the upright position of normal capsules It is checked in its development, and at the time of ripening it is nearly of the same length as in the beginning Many of them contain no good seeds at all from others I have succeeded in saving only a hundred seeds from thousands of capsules

These seeds if purely pollinated and with the exclusion of the visits of insects reproduce the variety entirely and without any reversion to the *lamarckiana* type

Correlated with the detailed structures is the form of the flower buds They lack the high stigma placed above the anthers which in

the *lamarckiana* by the vigorous growth of the style extends the calyx and renders the flower bud thinner and more slender Those of the *brevistylis* are therefore broader and more swollen It is quite easy to distinguish the individuals by this striking character alone although it differs from the parent in other particulars

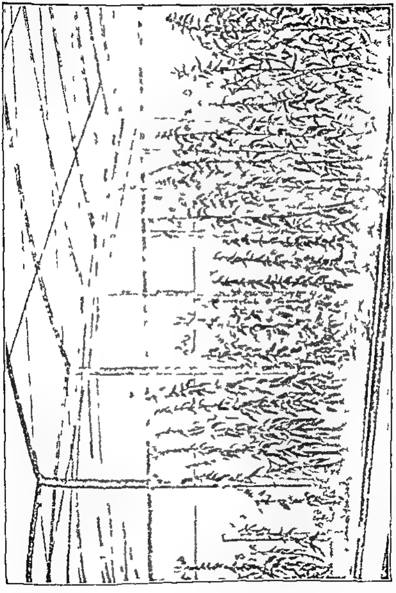
The leaves of the *O brevistylis* are more rounded at the tip, but the difference is only pronounced at times slightly in the adult rosettes but more clearly on the growing summits of the stems and branches By this character the plants may be discerned among the others some weeks before the flowers begin to show themselves

But the character by which the plants may be most easily recognized from a distance in the field is the failure of the fruits They were found nearly every year in varying, but always small numbers

Leaving the short styled primrose we come now to the last of our group of retrograde varieties This is the *O nannella* or the dwarf and is a most attractive little plant It is very short of stature reaching often a height of only 20–30 cm or less than one fourth of that of the parent It commences flowering at a height of 10–15 cm, while the parent form often measures nearly a meter at this stage of its development Being so very dwarfed the large flowers are all the more striking They are hardly inferior to those of the *lamarckiana* and agree with them in structure When they fade away the spike is rapidly lengthened and often becomes much longer than the lower or vegetative part of the stem

The dwarfs are one of the most common mutations in my garden and were observed in the native locality and also grown from seeds saved there Once produced they are absolutely constant. I have tried many thousands of seeds from various dwarf mutants and never observed any trace of reversion to the *lamarckiana* type I have also cultivated them in successive generations with the same result. In a former lecture we have seen that contrary to the general run of horticultural belief varieties are as constant as the best species if kept free from hybrid admixtures This is a general rule and the exceptions or cases of atavism are extremely rare In this respect it is of great interest to observe that this constancy is not an acquired quality but is to be considered as innate because it is already fully developed at the very moment when the original mutation takes place

From its first leaves to the rosette period and through this to the lengthening of the stem the dwarfs are easily distinguished from any other of their congeners. The most remarkable feature is the shape



of the leaves. They are broader and shorter, and especially at the base they are broadened in such a way as to become apparently sessile. The stalk is very brittle and any rough treatment may cause the leaves to break off. The young seedlings are recognizable by the shape of the first two or three leaves and when more of them are produced the rosettes become dense and strikingly different from others. Later leaves are more nearly like the parent type, but the petioles remain short. The bases of the blades are frequently almost cordate the laminae themselves varying from oblong ovate to ovate in outline.

The stems are often quite unbranched, or branched only at the base of the spike. Strong secondary stems are a striking attribute of the *lamarckiana* parent, but they are lacking, or almost so in the dwarfs. The stem is straight and short, and this combined with the large crown of bright flowers makes the dwarfs eminently suitable for bed or border plants. Unfortunately they are very sensitive especially to wet weather.

Oenothera gigas and *O. rubrinervis* or the giant, and the red veined evening primroses are the names given to two robust and stout species which seem to be equal in vigor to the parent plant while diverging from it in striking characters. Both are true elementary species differentiated from *lamarckiana* in nearly all their organs and qualities but not showing any preponderating character of a retrograde nature. Their differences may be compared with those of the elementary species of other genera as for instance of *Draba*, or of violets as will be seen by their description.

The giant evening primrose though not taller in stature than *O. lamarckiana* deserves its name because it is so much stouter in all respects. The stems are robust, often with twice the diameter of *lamarckiana* throughout. The internodes are shorter and the leaves more numerous covering the stems with a denser foliage. This shortness of internodes extends itself to the spike and for this reason the flowers and fruits grow closer together than on the parent plant. Hence the crown of bright flowers opening each evening, is more dense and more strikingly brilliant so much the more so as the individual flowers are markedly larger than those of the parents. In connection with these characters the flower buds are seen to be much stouter than those of *lamarckiana*. The fruits attain only half the normal size, but are broader and contain fewer but larger seeds.

The *rubrinervis* is in many respects a counterpart to the *gigas* but its stature is more slender The spikes and flowers are those of the *lamarckiana*, but the bracts are narrower Red veins and red streaks on the fruits afford a striking differentiating mark though they are not absolutely lacking in the parent species A red hue may be seen on the calyx, and even the yellow color of the petals is somewhat deepened in the same way Young plants are often marked by the pale red tinge of the mid veins, but in adult rosettes or from lack of sunshine this hue is often very faint

The leaves are narrow and a curious feature of this species is the great brittleness of the leaves and stems especially on annual individuals, for example on those that make their stem and flowers in the first year High turgidity and weak development of the mechanical and supporting tissues are the anatomical cause of this deficiency the bast fibres showing thinner walls than those of the parent type under the microscope Young stems of *rubrinervis* may be broken off by a sharp stroke and show a smooth rupture across all the tissues while those of *lamarckiana* are very tough and strong

Both the giant and the red veined species are easily recognized in the ro ette-stage The very young seedlings of the latter are not clearly differentiated from the *lamarckiana* and often a dozen leaves are required before the difference may be seen Under ordinary circumstances the young plants must reach an age of about two months before it is pos ible to discern their characters or at least before these characters have become reliable enough to enable us to judge of each individual without doubt But the divergencies rapidly become greater The leaves of *O gigas* are broader of a deeper green the blade more sharply set off against the stalk the whole rosettes becoming stout and crowded with leaves Those of *O rubrinervis* on the contrary are thin of a paler green and with a silvery white surface the blades are elliptic often being only 2 cm or less in width They are acute at the apex and gradually narrowed into the petiole

It is quite evident that such pale narrow leaves must produce smaller quantities of organic food than the darker green and broad organs of the *gigas* Perhaps this fact is accountable partly at least for the more robust growth of the giant in the second year Perhaps also some relation exists between this difference in chemical activity and the tendency to become annual or biennial The *gigas* as a rule produces far more and the *rubrinervis* far less biennial plants than the *lamarckiana* Annual culture for the one is as unreliable as

biennial culture for the other *Rubrinervis* may be annual in apparently all specimens in sunny seasons, which would allow a large part of the *gigas* to remain in the state of rosettes during the entire first summer It would be very interesting to obtain a fuller insight into the relation of the length of life to other qualities but as yet the facts can only be detailed as they stand

Both of these stout species have been found quite constant from the very first moment of their appearance I have cultivated them from seed in large numbers, and they have never reverted to the *lamarckiana* From this they have inherited the mutability or the capacity of producing in their turn new mutants But they seem to have done so incompletely changing in the direction of more absolute constancy This was especially observed in the case of *rubrinervis* which is not of such rare occurrence as *O gigas* and which it has been possible to study in large numbers of individuals So for instance the red veins have never produced any dwarfs, notwithstanding they are produced very often by the parent type And in crossing experiments the red veins gave proof of the absence of a mutative capacity for their production

[Besides the mutants just described there occurred two weak forms that could survive only if reared under protection and would have failed to survive in nature Here we have a place for the action of natural selection but operating with mutations instead of with fluctuating variations These two mutants are "the whitish and the oblong leaved evening primroses or the *Oenothera albida* and *oblonga* '

All of the mutants so far mentioned are constant forms that breed true to type Certain other types were either incapable of being bred or else were decidedly inconstant *Oenothera lata* had only pistillate flowers and therefore could not be fertilized by pollen of the same mutant *Oenothera scintillans* and *O elliptica* are fertile to their own pollen but produce progeny only partly like the parent, the rest reverting to the original type, *Oenothera lamarckiana*]

SUMMARY OF DE VRIES S MUTATION THEORY

THOMAS HUNT MORGAN

We may now proceed to examine the evidence from which De Vries has been led to the general conclusions given in the preceding pages De Vries found at Hilversum near Amsterdam a locality

T H Morgan *Evolution and Adaptation* (1903) Used by special permission of the publishers The Macmillan Company

where a number of plants of the evening primrose, *Oenothera lamarckiana* grow in large numbers. This plant is an American form that has been imported into Europe. It often escapes from cultivation as is the case at Hilversum where for ten years it had been growing wild. Its rapid increase in numbers in the course of a few years may be one of the causes that has led to the appearance of a mutation period. The escaped plants showed fluctuating variations in nearly all of their organs. They also had produced a number of abnormal forms. Some of the plants came to maturity in one year, others in two, or in rare cases, in three years.

A year after the first finding of these plants De Vries observed two well-characterized forms which he at once recognized as new elementary species. One of these was *O. brevistylis*, which occurred only as female plants. The other new species was a smooth leafed form with a more beautiful foliage than *O. lamarckiana*. This is *O. laevifolia*. It was found that both of these new forms bred true from self-fertilized seeds. At first only a few specimens were found, each form in a particular part of the field, which looks as though each might have come from the seeds of a single plant.

These two new forms, as well as the common *O. lamarckiana*, were collected, and from these plants there have arisen the three groups of families of elementary species that De Vries has studied. In his garden other new forms also arose from those that had been brought under cultivation. The largest group and the most important one is that from the original *O. lamarckiana* form. The accompanying table shows the mutations that arose between 1887 and 1899 from these plants. The seeds were selected in each case from self-fertilized plants of the *lamarckiana* form, so that the new plants appearing in each horizontal line are the descendants in each generation of *lamarckiana* parents. It will be observed that the species *O. oblonga* appeared again and again in considerable numbers, and the same is true for several of the other forms also. Only the two species *O. gigas* and *O. scintillans* appeared very rarely (Fig. 77).

Thus De Vries had in his seven generations about fifty thousand plants and about eight hundred of these were mutations. When the flowers of the new forms were artificially fertilized with pollen from the flowers of the same plant, or of the same kind of plant, they gave rise to forms like themselves, thus showing that they are true elementary species. It is also a point of some interest to observe that all these forms differed from each other in a large number of particulars

Only one form, *O. scintillans*, that appeared eight times, is not constant as are the other species When self fertilized its seeds produce always three other forms, *O. scintillans*, *O. oblonga*, and *O. lamarckiana*. It differs in this respect from all the other elementary species which mutate not more than once in ten thousand individuals

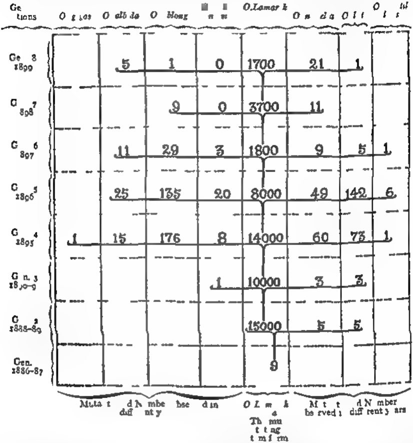


FIG 77—Diagram showing in condensed form the genealogy of the *Oenothera Lamarckiana* family and its various mutants during successive years The numbers under each type represent the number of new types observed each year (*From Tower*)

From the seeds of one of the new forms *O. laevifolia*, collected in the field plants were reared some of which were *O. lamarckiana* and others *O. laevifolia* They were allowed to grow together, and their descendants gave rise to the same forms found in the *lamarckiana*

family, described above, namely, *O lata, elliptica, nannella, rubri nervis*, and also two new species, *O spatu ala* and *leptocarpa*

In the *lata* family, only female flowers are produced and, there fore, in order to obtain seeds they were fertilized with pollen from other species Here also appeared some of the new species already mentioned, namely, *albida, nannella lata oblonga rubrinervis*, and also two new species *elliptica* and *subovata*

De Vries also watched the field from which the original forms were obtained, and found there many of the new species that appeared under cultivation The e were found however, only as weak young plants that rarely flowered Five of the new forms were seen either in the Hilversum field or else raised from seeds that had been collected there These facts show that the new species are not due to cultiva tion and that they arise year after year from the seeds of the parent form *O lamarckiana*

Conclusions —From the evidence given in the preceding pages it appears that the line between fluctuating variations and mutations may be sharply drawn If we assume that mutations have furnished the material for the process of evolution the whole problem appears in a different light from that in which it was placed by Darwin when he assumed that the fluctuating variations are the kind which give the material for evolution

From the point of view of the mutation theory species are no longer looked upon as having been slowly built up through the selec tion of individual variations but the elementary species at least appear at a single advance and fully formed This need not neces sarily mean that great changes have suddenly taken place and in this respect the mutation theory is in accord with Darwin s view that extreme forms that rarely appear sports have not furnished the material for the process of evolution

As De Vries has pointed out each mutation may be different from the parent form in only a light degree for each point although all the points may be different The most unique feature of these muta tions is the constancy with which the new form is inherited It is this fact, not previously fully appreciated that De Vries s work has brought prominently into the foreground There is another point of great interest in this connection Many of the groups that Darwin recognized as varieties correspond to the elementary species of De Vries These varieties Darwin thought are the first stages in the formations of species, and in fact, cannot be separated from species in most cases The main difference between the selection theory and

the mutation theory is that the one supposes these varieties to arise through selection of individual variations the other supposes that they have arisen spontaneously and at once from the original form The development of these varieties into new species is again supposed on the Darwinian theory, to be the result of further selection, on the mutation theory, the result of the appearance of new mutations

In consequence of this difference in the two theories it will not be difficult to show that the mutation theory escapes some of the gravest difficulties that the Darwinian theory has encountered Some of the advantages of the mutation theory may be briefly mentioned here

1 Since the mutations appear fully formed from the beginning, there is no difficulty in accounting for the incipient stages in the development of an organ and since the organ may persist, even when it has no value to the race, it may become further developed by later mutations and may come to have finally an important relation to the life of the individual

2 The new mutations may appear in large numbers, and of the different kinds those will persist that can get a foothold On account of the large number of times that the same mutations appear the danger of becoming swamped through crossing with the original form will be lessened in proportion to the number of new individuals that arise

3 If the time of reaching maturity in the new form is different from that in the parent forms then the new species will be kept from crossing with the parent form and since this new character will be present from the beginning the new form will have much better chances of surviving than if a difference in time of reaching maturity had to be gradually acquired

4 The new species that appear may be in some cases already adapted to live in a different environment from that occupied by the parent form and if so, it will be isolated from the beginning which will be an advantage in avoiding the bad effects of intercrossing

5 It is well known that the differences between related species consist largely in differences of unimportant organs and this is in harmony with the mutation theory, but one of the real difficulties of the selection theory

6 Useless or even slightly injurious characters may appear as mutations, and if they do not seriously affect the perpetuation of the race they may persist

LATER INVESTIGATIONS OF MUTATIONS

Since the publication of De Vries's classic investigations a large amount of attention has been paid both by botanists and by zoologists to the subject of mutations. Some of the investigators, notably B. M. Davis, went far toward discrediting the whole of the exceptionally careful work of De Vries by claiming that *Oenothera lamarckiana* is of hybrid origin. It was pointed out that the form worked with is a domestic type escaped from cultivation and that there is nowhere in the known world any wild species comparable with it. It is supposed to have been brought to Europe from America many years ago but there is no such species in America today. Davis claims that he has succeeded in producing, by crossing two American wild species, a hybrid form distinctly resembling *Oenothera lamarckiana* and that when inbred this hybrid produces offspring showing various combinations of the two parent species that are not unlike some of the mutants observed by De Vries. Jeffreys has also pointed out that the pollen grains of *Oenothera lamarckiana* exhibit a high percentage of sterility, which he believes to be a stigma of hybridity. The general tenor of this type of destructive criticism is to invalidate the whole mutation theory as developed by De Vries and to reduce his mutants to the level of mere Mendelian recombinations of characters once introduced from two or more parental species.

The large amount of work on the cytology of *Oenothera* by Gates and others has, however, served to show that the mutants of De Vries are more than hybrid segregates. Moreover, the beautiful work of Blakeslee on the Jimson weed (*Datura*) and the work of many other botanists, whose findings are reported by Gates in a contribution quoted below, serve to indicate that the type of evolutionary behavior first observed in *Oenothera* is by no means exceptional, but is probably a common thing at least among plants and may be commoner than we at present know in animals. It may be said by way of anticipation of Gates' detailed account that nearly all of the mutations observed in various species of plants may be definitely correlated with observable changes in the chromosomes of the germ cells, involving changes in number or changes in arrangement of these nuclear elements.

While the botanists busied themselves with their type of mutations the zoologists, especially T. H. Morgan and his able collaborators, were making discoveries of equal moment in connection with their studies of the mechanism of Mendelian heredity in *Drosophila*. As has al

ready been shown in previous chapters, hundreds of new hereditary types arose apparently spontaneously, in pure pedigreed stock Each new type is designated a mutant, and the cause of the changed hereditary condition is not a gross chromosomal change but an invisible change at a definite point in a definite chromosome, whose cause is unknown but whose location can be exactly determined Such mutations are known as gene mutations Like the mutants of *Oenothera* these *Drosophila* mutants do not differ from the parent species in just one or two characters but in several or many characters Usually some one or two characters in any given mutant are especially characteristic, and these serve to give a name to each mutant and make it easier to identify them Both morphological and physiological characters are involved in these mutants, and every part of the body may be involved Sometimes the change is so slight as to require an eye sensitized by much training to detect them It may happen for example that two mutants of the eye are so much alike that the human eye is not sufficiently keen to tell them apart, but they may be distinguished by differences in their hereditary behavior A large percentage of the mutants discovered in *Drosophila* are lethals,' which means that the change is decidedly for the worse under the prevailing conditions of life and that they render the individual unfit to live Possibly under decidedly different conditions some of these lethal mutants might be better adapted than the normal individuals A further discussion of the rôle of mutants in evolution will be given in a later connection

The following two rather technical, but very interesting, discussions as to the nature, causes and significance of mutations are from two men who are recognized as perhaps the leaders in the two branches of mutation study R R Gates has done a large amount of important work especially upon the cytology of *Oenothera* and H J Muller has done and is still doing much to enrich our understanding of the mutational phenomena exhibited by *Drosophila* While these two workers do not agree as to the relative emphasis that should be placed upon the two types of mutation, it is obvious that both types are of very great importance in evolution

THE NEO-MUTATIONIST POSITION

R RUGGLES GATES

Since the original work of De Vries the subject of mutation in Oenothera has advanced in many directions and the explanation of the phenomena has taken on various aspects Mutation has become

essentially a cell problem. Cytological investigations have shown that many of the mutations are concerned with new chromosome numbers, and the precise nature of the change which has led to the appearance of forms with a new number is known with more or less certainty in the various cases. The new number is in each case present throughout the plant and will be found whether the chromosomes be counted in growing petals, root tips or anthers. These discoveries led in 1915 to the conception that each mutation with its new external characters is the result of nuclear changes transmitted by mitosis to every cell of the plant during development. A fundamental advance in the analysis of mutations has thus been made

Mutations can now be classified into two types. (1) Mutations which are inherited as Mendelian differences and which may be looked upon provisionally as the result of a chemical change in one gene or locus of a chromosome The great majority of the mutations in Drosophila are of this type. On the other hand very few Mendelian mutations are known in Oenothera. The two best known are *rubricalyx* which is a dominant in crosses and *brevistylis* which is inherited as a recessive. (2) Mutations resulting from a visible nuclear change involving a new number of chromosomes. Probably the majority of Oenothera mutations belong here Similar mutations have been discovered in Drosophila and also in Datura Examination of the chromosome numbers in related species of wild and cultivated plants shows that such changes have been of relatively frequent occurrence in the evolution of many plant genera but they appear to be less common in animals.

CHROMOSOME MUTATIONS

The mutations with new chromosome numbers which are particularly characteristic of Oenothera may be classified into three types —(1) *trisomic forms* i e mutations with one or sometimes two extra chromosomes ($2n+1$) (2) *triploid* forms ($3n$) and (3) *tetraploid* ($4n$) forms. Other forms with different numbers as 20 or 30 may be regarded as derivatives from these types

Trisomic forms are known to arise through non disjunction or a reduction division in which both members of one pair of chromosomes enter the same daughter nucleus The best known mutation of this kind is *Oenothera lata* with 15 chromosomes (*O lamarckiana* having 14) But a number of others are now known including *scintillans albida oblonga subovata* and more recently *cana pallescens, lata* and *liquida* Several other derivatives of *Oenothera lamarckiana* are also from their behavior almost certainly trisomic When p[illegible]

from *O lamarckiana* they give the two parental types of offspring having presumably 14 and 15 chromosomes Since there are only seven pairs of chromosomes these trisomic types can not all be accounted for by duplication of a different chromosome in each case

The genetic relationships between these trisomic mutants are also interesting and peculiar Thus *lata* can give rise to *scintillans* in its offspring, and *scintillans* can similarly produce *lata* Also *lata* (pollinated from *lamarckiana*) can give rise to several other trisomic mutations Many of these relationships can be explained by the assumption of double non disjunction i e both members of one chromosome pair entering one germ cell while both members of another pair enter the opposite cell It is highly probable that such cases occur Thus germ cells would be produced with the chromosome content AACDEFG and BBCDEFG It can be shown that by such a process one trisomic mutation could give rise to another in its offspring It is very probable that *lata* is a primary trisomic mutation e g $\frac{\text{AABCDEFG}}{\text{ABCDEFG}}$ i e, with three A chromosomes, while some other trisomic $(2n+1)$ mutations are probably secondary e g, $\frac{\text{AABCDEFG}}{\text{ACCDEFG}}$ i e with for example three A and three C chromosomes but only one B chromosome All such irregular chromosome distributions are probably enabled to occur through a weakness in the attraction which normally leads to close pairing of homologous chromosomes during synapsis or on the heterotypic spindle There is much evidence of variation in the strength of this attraction in Oenothera

Cleland has recently found that the chromosomes in various Oenothera species retain their end to-end connections even on the heterotypic spindle He has also shown that in several species the arrangement of the chromosomes is more or less constant and characteristic during the stages immediately preceding the reduction division Thus in *O franciscana* four of the chromosomes form a ring while the other ten are arranged in five ring pairs which are at first linked to the circle of four in a definite way In a form called *O franciscana sulphurea*, which is derived from *O biennis*×*franciscana* 12 chromosomes end to-end form a circle and the other two form a pair which is at first linked round the larger chain of 12, and this arrangement is said to be constant Thus in the derived form a rearrangement of the chromosomes with relation to each other has taken place Cleland finds similar fixed arrangements in other species.

Thus in a race identified with *O muricata* the 14 chromosomes all form a single circle in *O biennis* they are usually in two interlooking circles one with 6 and the other with 8 chromosomes while in the mutant *oblonga* with 15 chromosomes the arrangement is more variable but frequently shows a ring of 5 single chromosomes with 5 pairs attached to it In a trisomic mutant from *O rubricalys*×*hewettii* a varying number of ring pairs was found by the writer If the relative con stancy of these arrangements is confirmed it will show an essentially new type of integration in nuclear structure that is a fixed positional arrangement of the chromosomes in the nucleus with relation to one another This will also confirm the hypothesis of the writer years ago that the homologous maternal and paternal chromosomes in Oenothera are usually arranged alternately on the spireme thread before the reduction division The fact that also, as observed by the writer in 1908 pairs of chromosomes are frequently detached from the rest of the spireme in certain forms at an early stage of diakinesis would make it easier for double non-disjunction to occur on the heterotypic spindle in these forms The further study of the chromosome arrangements in hybrids and mutants will throw more light on these rearrangements and perhaps also on the nature of the forces which bring them about Such rearrangements without change of number if they prove to be constant are to be considered as mutations of another kind

Whether non disjunction has played a part in the appearance of species in nature with a different chromosome number is as yet un certain But there are certain genera such as Carex in which the haploid numbers usually increase by one from species to species Heilborn suggests that this may have happened by non-disjunction as in *Oenothera lata* followed by the division of the extra chromosome to form a pair

Polyploidy —An increase in the chromosome number by multiples of the haploid number (polyploidy) is a phenomenon of considerable phylogenetic significance in plants although it appears to be relatively uncommon in animals There has been a burst of new knowledge on this subject in the last few years Since the original mutant *Oenothera gigas* has been shown to be tetraploid and *semigigas* mutations triploid we have an experimental basis for the interpretation of all such cases It appears probable that the triploid condition in Oenothera arises through the union of two male nuclei with the egg as this condition has been actually observed in *O lamarckiana* by Ishikawa and in other plants as well

A difference of opinion has long existed as to whether *O gigas* arose from the fusion of two diploid cells or from a suspended mitosis with division of the chromosomes in the fertilized egg I am still inclined to adhere to the latter view as more probable with perhaps a sudden lowering of temperature just after fertilization as the cause Although it is a fact that diploid germ cells do sometimes occur diploid pollen grains are not known to be viable in plants

The frequency of polyploidy in flowering plants and also in other groups of plants is one of the surprises of recent years Not only does the condition occur in such cultivated plants as pineapples, bananas mulberries, wheat oats sugar cane, dahlias, and tobacco, but also in such genera of wild plants as the roses maples, chrysanthemums, Erigeron Hieracium, Rumex, Rubus Crataegus Spiranthus, and a number of others The multiplication of chromosome sets runs as high as $8n$ in Rosa and in Acer and even as high as $10n$ in certain species of Rumex (80 chromosomes) and chrysanthemums (90 chromosomes) Such a widespread phenomenon must be of fundamental significance in the evolution of the genera in which it occurs The higher degrees of polyploidy are probably often connected with hybridization but there the higher chromosome numbers are usually accompanied by apogamous (asexual) reproduction which renders constant even forms with an unbalanced chromosome number This is true even of the triploid mulberries and Erigerons, etc In every case of polyploidy the higher numbers have not arisen gradually by the addition of single chromosomes, but one or more complete sets have been added each time and the process is a mutation involving considerable discontinuity

That still other kinds of chromosome change occur, is shown both from experimental work and by comparison of the chromosomes of related species Thus transverse segmentation of all chromosomes has taken place in *Primula kewensis*, and end to-end fusion of certain pairs has evidently occurred in some species of Drosophila In the Japanese violets there is some indication that the small number of large chromosomes in certain species may have been derived by the fusion of smaller chromosomes found in other species A process suggesting transverse fragmentation of certain pairs of long chromosomes appears to have occurred in various genera of Liliaceae Further study will no doubt throw light on the nature of these processes It appears already that the passage from one genus to another has not infrequently been marked by a visible change in the chromatin mor

phology of the nucleus . Such alterations in the conformation of the nuclear material are to be regarded as germinal changes even though they are not accompanied by external changes in the organism

MUTATION

H J MULLER

Beneath the imposing building called Heredity there has been a dingy basement called Mutation Lately the searchlight of genetic analysis has thrown a flood of illumination into many of the dark recesses there revealing some of them as ordinary rooms in no wise different from those upstairs, that merely need to have their blinds flung back while others are seen to be subterranean passageways of quite a different type In other words, the term mutation originally included a number of distinct phenomena which from a genetic point of view, have nothing in common with one another They were classed together merely because they all involved the sudden appearance of a new genetic type Some have been found to be special cases of Mendelian recombination some to be due to abnormalities in the distribution of entire chromosomes and others to consist in changes in the individual genes or hereditary units It seems incumbent upon us however in the interests of scientific clarity to agree to confine our use of the term mutation to one coherent class of events The usage most serviceable for our modern purpose would be to limit the meaning of the term to the cases of the third type—that is to real changes in the gene This would also be most in conformity with the spirit of the original usage for even in the earlier days mutations were conceived of as fundamental changes in the hereditary constitution and there were never intentionally included among them cases merely involving redistribution of hereditary units—when these cases were recognizable as such In accordance with these considerations our new definition would be , 'mutation is alteration of the gene And alteration as here used is of course understood to mean a change of a transmissible or at least of a propagable sort

In thus trimming down the scope of our category of mutation we do not deprive it of the material of most fundamental evolutionary significance For all changes due to the redistribution of individual genes or of groups of genes into new combinations proportions or quantities are obviously made possible only by the prior changes tha

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make these genes differ from each other in the first place It should in addition be noted that changes due merely to differences in the gross proportions of entire groups of genes must be relatively incapable of that delicate adjustment which is required for evolutionary adaptation And as to the question frequently raised whether all evolution is ultimately due to mutation, this is necessarily answered in the affirmative by our definitions of the gene and of mutation, which designate the gene as any unit of heredity, and mutation as any transmissible change occurring in the gene The question of the basic mechanism of evolution thus becomes transferred to the problem of the character, frequency, and mode of occurrence of mutation taken in this precise, yet comprehensive sense And since eugenics is a special branch of evolutionary science it must be equally concerned with this problem

In choosing the body of data wherewith to attack these questions of mutation in their new form it must unfortunately be recognized that the results with the evening primrose, Oenothera, although they formed the backbone of the earlier mutation theory, can no longer be regarded as having a direct bearing on the modern problem since they cannot be shown to be due directly to changes in the genes Certain of them, such as gigas lata scintillans etc, have been proved by Geerts, Lutz Gates, and others to be due to abnormalities in the apportionment of the chromosomes Very valuable information on the genetics of cases of this sort is now being obtained especially in the work of Blakeslee Belling, and Farnham on much clearer cases of similar character in the Jimson weed and finally in the work of Bridges on the fruit fly Drosophila Most of the other so-called mutations in the evening primrose appear to be due to the normal hereditary processes of segregation and crossing over working on a genetic constitution of a special type Evidence for this was obtained in my analysis of the analogous case existing in the fly Drosophila, as follows It had previously been shown by de Vries, and further elaborated by Renner that germ cells or individuals of Oenothera bearing certain genes always died in such a way that all the surviving individuals were heterozygous (hybrid) in regard to these genes I later showed through work on Drosophila, that when such a condition (there called 'balanced lethal factors) exists, the situation tends to become still further complicated through the presence of other heterozygous genes which are linked to those which cause death When one or a group of these non lethal genes crosses over (separates) from the lethals, as they occasionally do they may become homozygous producing a visible effect Thus new types of individuals appear which may be ascribed to "mutation,' whereas they

are really due to crossing over. The work of Frost on stocks has shown that a precisely analogous situation exists in that form also and G H Shull is obtaining direct evidence for the same conclusion in the evening primrose itself. In any event, it must be granted that so long as this interpretation cannot be definitely refuted these variations can not be used as examples on which to base our theory of gene change. In place then of the elaborate system of conclusions which has derived its support chiefly from the results in the evening primrose it will be necessary for our present theory of gene change to erect an independent structure *built upon an entirely new basis*.

The data upon which the new theory must be built consist of two main sorts which may be called direct and indirect. (1) In the cases giving the direct evidence, the occurrence of the gene change can be proved, and it is possible to exclude definitely all alternative explanations such as contamination of the material emergence of previously latent factors non-disjunction etc. So far the only considerable body of such evidence is that gotten in the Drosophila work where mutations have (in this sense) been actually observed in at least 100 loci. Considered collectively however there exist in other organisms enough scattered data to afford ample corroborative evidence for the generality of occurrence of mutations like those observed in the Drosophila work. In addition several specially mutable genes have been found in a number of plants (as well as in Drosophila) that are giving highly valuable information along their particular lines. And a number of selection experiments that have been performed on non segregating lines of various organisms have also given us direct evidence if not of the *frequency then at least of the infrequency* of mutations. (2) As for the indirect data these may be gotten by examination of Mendelian factor-differences of all kinds on the assumption that they must have arisen through mutation. Although this assumption can be shown to be fully justified these cases cannot provide information concerning the manner of origin of the mutants nor can they furnish a reliable index of the frequency of mutations since the mutant genes may have been subjected to an unknown amount of selective elimination or selective propagation before the observations were taken. As for the still more indirect data, derived from studies of phylogenetic series and comparisons between different species genera etc. these occasionally give suggestive results but where crosses cannot be made or where the differences cannot be traced down to the individual genes, such facts can seldom lead to trustworthy genetic conclusions.

On these various data, duly weighted we may found our new muta

tion theory We know nothing as yet, about the mechanism of mutation, or about the nature of the gene—aside from the fact that nearly all genes hitherto studied behave like material particles existing in the chromosomes Nevertheless there is already evidence for a number of empirical principles regarding the changes of the genes, some of which may conveniently be listed here in the form of 14 statements I shall have opportunity merely to present these principles, without attempting any adequate explanations of how they have been derived from the data

1 The first and probably most important principle is that most genes—both mutant and normal —are exceedingly stable Some idea of the degree of this stability may be obtained from some quantitative studies of mutation which Altenburg and I have made in the fruit fly Drosophila It may be calculated from these experiments that a large proportion of the genes in Drosophila must have a stability which—at a minimum value—is comparable with that of radium atoms Radium atoms, it may be recalled have a so-called 'mean life of about two thousand years

2 Certain genes are however vastly more mutable than others For example a gene causing variegation in corn studied by Emerson and another in the four o clock, studied by Maryatt ordinarily have a mean life of only a few years and that causing bar eye in Drosophila has a mean life of only about 65 years as is shown by the results of Zeleny (In expressing these results we are here using the physicists index of stability which seems most appropriate for the present purpo e also)

3 External agents do not ordinarily increase the mutability sufficiently (if at all) to cause an obvious "production' of mutation

4 The changes are not exclusively of the character of losses this is shown by the well established occurrence of reverse mutations in bar-eyed and white eyed Drosophila in Blakeslee s dwarf Portulaca, Emerson s variegated corn, and probably in a number of other recorded instances It is known that mutations having an effect similar to that of losses do occur however, and they may be relatively frequent

5 The change in a given gene is not in all cases in the same direction, and it does not even, in all cases involve the same characters The latter point is illustrated by a series of mutations which I am investigating in Drosophila which all involve one gene but which produce, as the case may be either a shortened wing an eruption on the thorax a lethal effect or any combination of these three

6 The direction of mutation in a given gene is however, preferential occurring oftener in some directions than in others. This is well illustrated in the studies on variegated corn and four-o clocks and on the bar eye and white eye and other series in Drosophila

7 The mutability and preferential direction may themselves become changed through mutation as illustrated by some of the same cases.

8 The mutations do not ordinarily occur in two or more different genes at once In only two instances in Drosophila have mutations been found in two different separated genes in the same line of cell of one individual. But a recurrent case apparently of this kind has recently been described in oats by Nilsson Ehle

9 Not only does the mutation usually involve but one kind of gene—it usually involves but one gene of that kind in the cell. That is the allelomorphs mutate independently of one another just as totally different genes do There is evidence for this derived from corn Portulaca and Drosophila

10 Mutations are not limited in their time of occurrence to any particular period of the life history This has been proved in the above mentioned studies on mutable plants in Drosophila and in other cases

11 Genes normal to the species tend to have more dominance than the mutant genes arising from them This is very markedly the case in Drosophila, where even the relatively few mutant genes that have been called dominant are very incompletely so and might more justly be called recessive In other organisms the same condition of things is *strongly suggested although the direct data on occurrence of muta*tions is as yet too meagre to allow of certainty

12 Most mutations are deleterious in their effects This applies not only to the organism as a whole but also to the development of any particular part the delicate mechanisms for producing characters are more likely to be upset than strengthened so that mutations should more often result in apparent losses or retrogressions than in progressive changes This is both an a priori expectation and a phenomenon generally observed

13 Mutations with slight effects are probably more frequent than those with more marked effects . This must not be understood as referring to the different mutations of each given gene but it applies in a comparison of the mutations occurring in different genes Thus there

Contiguous genes may be affected in the rare cases known as "deficiencies found by Bridges and Mohr

are more than a dozen mutations in different loci which reduce the size of the wing in Dro ophila so slightly a to leave it more than half its original length, whereas only four reduce it to less than half length Mutant genes with effects so slight as to be visible only by the aid of specific co-genes seem to arise still more frequently It ■ reasonable to conclude that the mutations with slighter effects would more often take part in evolution, because they should usually be less deleterious and this conclusion is born out by observations on the multiplicity with which such factor differences with relatively slight effects are found in species crosses

14 The range of those mutations which are of appropriate magni tude to be visible is probably very small in comparison with the entire spectrum of mutations so that there are many more lethals than visible mutations and probably more subliminal than visible

The above empirical and semi empirical principles must be re garded as a mere preliminary scaffolding, for the erection of a later more substantial theory of mutation Time does not permit me here to discuss which directions of research, and what methods, seem the most promising for future results Suffice it to say that it is especially important to obtain accurate data concerning the effect of various conditions upon the rate of mutation This seems one of the logical routes by which to work towards the artificial production of mutation and consequent more perfect control of evolution At the same time such results should also give a further insight into the structure of the gene The way is now open for the fir t time to such studies on mutation rate first through the finding, by Emerson, Baur Maryatt Zeleny and Blakeslee of a number of specially mutable factors in different organisms and second, through certain special genetic meth ods which I have elaborated in Drosophila for the detection of lethal and other mutations there

It has now become recognized that advances in theoretical or pure science eventually carry in their train changes in practice of the most far reaching nature—changes which are usually far more radical than tho e caused by progress in the applied science directly concerned It may therefore be asked at this point by eugenists ' Are there any applications of the knowledge which has already been gained about mutation in general to eugenics and to the principles which should govern us in guiding human reproduction? I think that one such application is already clearly indicated

In order to understand the nature of this application it will be nec

essary first to consider the proposition—emphasized by East and Jones in their book "Inbreeding and Cross breeding —that the only way for a genetically sound stock to be formed is by its going through a course of inbreeding with elimination by natural or artificial selection of the undesirable individuals that appear in the course of this inbreeding The truth of this proposition depends upon the fact that many recessive genes of undesirable character are apt to exist in a population Since the frequency with which these genes are able to produce their characteristic effects i e to come to light depends on *the closeness of the inbreeding* it is evident *that inbreeding will be* necessary in order to recognize the genes adequately and hence to eliminate them

Our present theory of mutation however carries us further than the proposition just considered It shows that these undesirable genes have arisen by mutation in fact, as stated in point 12 the *great majority* of mutations are deleterious probably even to the degree of being lethal and it is also known as noted in point 11 that many—probably the great majority—are recessive In other words our mutation theory shows that probably the majority of the mutations that are occurring are giving rise to genes of just the type specified in the above discussion This immediately shows us that not only are inbreeding and selection desirable for raising the genetic level of a population, but they are absolutely necessary merely in order to maintain it at its present standard For the same process of mutation which was responsible for the origination of these undesirable genes in the past must be producing them now and will continue to produce them in the future Therefore without selection or without the inbreeding that makes effective selection possible these lethals and other undesirable genes will inevitably accumulate until the germ plasm becomes so riddled through with defect that pure lines cannot be obtained and progress through selection of desirable recessive traits can never more be effected since each of them will have become tied up with a lethal To avoid such a complete and permanent collapse of the evolutionary process it is accordingly necessary for man or nature to resort to a periodically repeated although not continuous series of inbreedings and selections in the case of any biparental organism

This conclusion is more than a mere speculation or even a deduction from our principles The reality of this process of mutational deterioration has been directly proved in the case of Drosophila through experiments that I have conducted on lines in which the

processes that are essential for the effectiveness of inbreeding and selection were prevented in these lines there was found an accumulation of lethal genes so rapid that it would have taken but a few decades to have brought about the presence of a lethal gene in practically every chromosome of every fly Although the same general thesis undoubtedly applies also to mankind we do not yet know the speed of the process here Its speed depends upon the actual frequency of mutations, which it will be very important—and extremely difficult—to determine in the case of mankind Meanwhile, no matter what this rate may be the process remains a real one, which must eventually be reckoned with and either grappled in time, and conquered, or else yielded to

I have dwelt at length upon this particular application to eugenics, of some of the mutation studies I believe, however that this is but one example of such applications, and that from an increasing knowledge of our theoretical science there will inevitably flow an increasingly adequate technique for coping with our refractory human material Meanwhile, the crying need is for more of the theoretical knowledge—and for the support of pure science in its investigation of the processes lying at the root of the germ plasm

THE CAUSES OF MUTATIONS

In attempting to determine the causes of the appearance of new hereditary characters we must first of all learn which of the categories of variation we are dealing with If we find that a so-called mutant has a different number or arrangement of chromosomes, we may say that this change in the chromosomes is the cause of the somatic differences seen in the mutant for it would be strange if a relatively large change in the hereditary material did not affect the somatic expression of specific characters As has already been suggested by Gates the cause of chromosomal aberrations may be environmental, as for example sudden lowering of temperature during critical periods of the germ cell cycle We have, however, no controlled experiments that prove this to be the case Again, there is a tendency to account for non-disjunction and other types of chromosomal aberration through purely internal causes, such as weakness of attraction between homologous chromosomes resulting in a failure of synapsis In general it may be said that apart from being able to note a definite correlation between a changed somatic condition and a changed chromosomal

condition we do not know very much about the causes of chromosomal mutations

The causes of gene mutations in *Drosophila* have remained until recently a complete mystery Muller had been able very slightly to increase the rate of mutation by raising the temperature of fly cultures but he was not completely satisfied with these results In 19 6 how ever he startled the scientific world by the announcement that he had been able by exposing adult animals to fairly heavy doses of X rays vastly to accelerate the rate of mutations Where some gene muta tion occurred under normal conditions in only about 1 in 300 gametes the X rays raised this ratio to 1 in 2 gametes an increase of 150 per cent All of the old familiar mutations that had been occurring in untreated cultures were induced in much larger numbers by X rays but only a very few new mutations were produced It seems that the X ray acts merely as a catalyst hastening a process that would go on slowly without such an agent Numerous experimenters have fol lowed Muller s lead in the use of X rays as an agent for accelerating the rate of mutations Muller has proposed a general theory that the ordinary so-called spontaneous mutation of genes may be due to the presence of minute amounts of radio active substances accumulated in the tissues of plants and animals This theory seems somewhat far fetched at the present writing We are still in almost complete ignorance as to the causes of gene mutations and probably shall con tinue to be in ignorance until we gain some more accurate information as to the exact physical and chemical nature of genes and how they act in producing character differences

MUTATION AND EVOLUTION

T H MORGAN

What bearing has the appearance of these new types of Drosophila on the theory of evolution may be asked The objection has been raised in fact that in the breeding work with Drosophila we are dealing with artificial and unnatural conditions It has been more than im plied that the results obtained from the breeding pen the seed pan the flower pot and the milk bottle [used as breeding container for *Droso phila*] do not apply to evolution in the open nature ' at large or to wild types To be consistent, this same objection should be extended to the use of the spectroscope in the study of the evolution

From *A Critique of the Theory of Evolution* Princeton University Press 1916

of the stars to the use of the test tube and the balance by the chemist and of the galvanometer by the physicist All these are unnatural instruments used to torture Nature s secrets from her I venture to think that the real antithesis is not between unnatural and natural treatment of Nature but rather between controlled or verifiable data on the one hand, and unrestrained generalization on the other

If a systematist were asked whether these new races of Drosophila are comparable to wild species he would not hesitate for a moment He would call them all one species If he were asked why, he would say, I think These races differ only in one or two striking points, while in a hundred other respects they are identical even to the minutest details He would add that as large a group of wild flies would show on the whole the reverse relations, *viz*, they would differ in nearly every detail and be identical in only a few points In all this I entirely agree with the systematist for I do not think such a group of types differing by one character each, is comparable to most wild groups of species because the difference between wild species is due to a large number of such single differences The characters that have been accumulated in wild species are of significance in the maintenance of the species or at least we are led to infer that even though the visible character we attend to may not itself be important one at least of the other effects of the factors that represent these characters is significant It is, of course hardly to be expected that *any* random change in as complex a mechanism as an insect would improve the mechanism, and as a matter of fact it is doubtful whether any of the mutant types so far discovered are better adapted to those conditions to which a fly of this structure and habitat is already adjusted But this is beside the mark, for modern genetics shows very positively that adaptive characters are inherited in exactly the same way as are those that are not adaptive and I have already pointed out that we cannot study a single mutant factor without at the same time studying one of the factors responsible for normal characters for the two together constitute the Mendelian pair

And finally I want to urge upon your attention another question Evolution of wild species appears to have taken place by modifying and improving bit by bit the structures and habits that the animal or plant already possessed We have seen that there are thirty mutant factors at least that have an influence on eye color, and it is probable that there are at least as many normal factors that are involved in the production of the red eye of the wild fly

Evolution from this point of view has consisted largely in introducing new factors that influence characters already present in the animal or plant

Such a view gives us a somewhat different picture of the process of evolution from the old idea of a ferocious struggle between individuals of a species with the survival of the fittest and the annihilation of the less fit Evolution assumes a more peaceful aspect. New and advantageous characters survive by incorporating themselves into the race, improving it and opening to it new opportunities In other words the emphasis may be placed less on the competition between the individuals of a species (because the destruction of the less fit does not *in itself* lead to anything that is new) than on the appearance of new characters and modifications of old characters that become incorporated in the species for on those depend the evolution of the race

CHAPTER XXVII

GUIDING FACTORS INTRODUCTION

Preliminary discussion —All of the factors hitherto discussed appear to operate on a random basis obedient to the laws of pure chance Of themselves then they might be conceived of as producing a high degree of diversity and innumerable novelties, but that would be all If there is something of orderliness something of direction, something adaptive, something progressive, or even something purposive about evolution, there should be guiding factors responsible for each and all of them

The extent to which guiding factors are a necessary part of the evolutionary mechanism depends upon the extent to which there actually exist in nature conditions that cannot be accounted for on a purely random basis Guiding or directing factors imply goals objectives definite trends improvements of one sort or another What is there about nature that seems to require a guiding hand?

Adaptations —One of the marvels of life is that the organism and the environment seem so well adapted to each other that the particular organs of an individual seem so well designed to perform their many and varied functions that the various species are so nicely adjusted to one another in any given natural community that each seems to be a strand in an intricate and delicately adjusted web of life One of the most important goals or objectives of evolution then must be adaptation We are using these terms goals and 'objectives' without implying any teleological considerations though why there may *not be purpose in nature I do not know At least it is better* for the scientist to shy away from any taint of teleology So let us assume that adaptation is one of the main objectives of evolution using the term 'objective only to imply that evolutionary processes somehow, by devious paths, seem to arrive at various degrees of fitness The mechanism bringing about this fitness may be blind and may vision no goal but it gets there just the same

Since adaptation is so intimately associated with evolution—in fact one of its principal attributes—it will be necessary to take a short excursion into natural history in order that we may come to realize at least some of the facts of adaptation that confront the evolutionist

and that challenge explanation The following chapter on "Adaptation in Nature" is frankly an interpolation but an essential one unless the student be already well informed in this field Also the chapter on "The Web of Life" is necessary if we are to avoid thinking of species as isolated entities The evolution of a species always takes place in a natural setting part of which consists of the lifeless environment and part of which consists of its animal and plant neighbors

Orthogenetic trends—Various kinds of definitely directed evolutionary trends have been described Sometimes these trends concern themselves with such relatively trivial characters as the intricate markings on the shells of mollusks and brachiopods sometimes they have to do with the horns of elks or of titanotheres and sometimes they concern the toes and teeth of the horse family One striking feature of these so-called "orthogenetic" series is that the trends have not always culminated in a condition of maximum efficiency but have sometimes gone beyond this point and have become positively detrimental in some cases even contributing to the extinction of the species possessing them If there is some guiding factor other than natural selection that tends to push evolutionary changes forward in definite paths such a force might be responsible for adaptive trends as well as the non adaptive ones In general however it may be said in advance of the more detailed discussion of this question in a later chapter that most geneticists are either skeptical of the existence of any very definite orthogenesis, or else consider it explainable through natural selection

Progressive evolution—It is generally assumed that "evolution" and "progress" are synonymous terms It is claimed that forms of life now living are on the whole "more advanced" than those that have lived in earlier times and that there has been a steady advance throughout the ages But what do we mean by progress in evolution or by more or less advanced forms? Progress and advance imply both direction and a goal or goals What are the goals toward which evolution is progressing?

Some claim that the final goal of life is perfect adaptation of all living things to the environment and to one another But is there any evidence that life today is any better adapted than was life in Cambrian times? Is there any ground for assuming that man is any better adapted to the environment than is the *Amoeba*? Man is adapted to a much more complex environment than is the *Amoeba* but is he any better adapted to the human environment than is *Amoeba* to the amoeban environment? I see no reason for assuming that there is any difference

in the degree of perfection of adaptation in these two widely different species each highly successful in its own milieu and each cosmopolitan in distribution In view of such considerations as these it is not easy to maintain that evolution is a process of becoming better and better adapted

Specialization.—Various other criteria of progress have been suggested One of these is *specialization* Are the most highly specialized organisms more advanced than the less specialized? Are the more specialized ones closer to the ultimate ideal goal of evolution than the more generalized? Now many of the most intensely specialized types of organisms are the parasites that have in many cases undergone degeneration of sense organs locomotor structures, and even digestive systems, but have developed specialized structures making it possible for them to live and thrive in some particular system of some species of host animal Here is specialization carried to extremes but is it progress? I believe it is and for the following reasons

A primary objective of living organisms is that of exploiting to the fullest possible extent the energy resources of the world Ultimate success will be attained only when no further energy resources remain to be exploited Now the sources of energy are many and varied and each different energy source requires a different type of energy-exploiting equipment Progress in specialization would therefore involve the evolution of as many highly specialized types of organisms as there are highly specialized energy sources Thus there is a very real value for life as a whole in the production of numerous highly specialized forms even though some be from the morphological viewpoint degenerate and degraded parasites

Another type of specialization that has had a long and steady progressive evolution is the specialization of parts of the single organism for the performance of varied bodily functions This type of specialization is commonly called division of labor" In the course of animal evolution this specialization of parts begins at the lowest level in the Protozoa where portions of the protoplasm are specialized to form organelles of various kinds each kind performing its own special function Among the lower Metazoa such as Coelenterata and Platyhelminthes we have a new level of organization built up of aggregates of units each equivalent in a sense to a whole protozoan individual In these multicellular individuals division of labor is accomplished by specializing the cell units for different functions, with a corresponding increase in general efficiency of the individual

Among segmental organisms we have another advance in bodily specialization Here chains of individuals each in a sense morphologically equivalent to a single individual of the flatworm type become welded together into more complex segmented organisms With this new level of complexity of organization comes the possibility of specializing different segments each of them equivalent to a whole individual of the lower grade for particular functions Some perform chiefly nervous and sensory functions others reproductive functions and still others respiratory or digestive functions Each segment in certain parts of the body becomes a specialist in some one function which it performs more efficiently when relieved of some of the other functions Of course specialization would be of no value unless integration and interdependence of part upon part kept pace with it Hence one of the results of the trends just described is the closer integration of parts and the greater definiteness of individuality

Even among segmental organisms as for example the ants and bees division of labor takes place among segmental individuals and a new and higher level of organization—social organization—emerges Here in these insect societies individuals are specialized in several ways some become functional males and females others (immature females) become specialized as workers or protective units known as soldiers Thus a society is in a sense a fairly definitely integrated individual of a higher level involving a high degree of interdependence of the various kinds of specialists upon one another The integrating factor seems to be associated with the family relationship of all members of a given colony All members of a given colony are offspring of the same mother and father They are extremely clannish and resent vigorously any intrusion by outsiders

It therefore appears that one of the principal progressive trends of evolution is one in which units of lower orders are aggregated into complex units of higher orders Each aggregate is a new type of individual with new properties not entirely the result of a summation of the properties of the ingredient units This idea has sometimes been spoken of as *emergent evolution* according to which with each higher level of units new properties of the whole emerge which are more than the sum of properties of the parts This might also be thought of as a kind of creation for something new comes into being as though out of nothing

While the foregoing discussion is in a sense a digression it seems well to call attention somewhere in a book on evolution to these facts

and theories The facts are there for us to explain and the theories are attracting so much attention at present that they should not be ignored

Increase in size is one of the commonest trends of evolution but is size increase progress? Many great groups of organisms have from age to age steadily increased in size of individuals Many fossil pedigrees show clearly that size increase is one of the steadiest of progressive trends But size if carried to extremes is disadvantageous witness the complete extinction of the ancient dinosaurs and the rapidly progressing extinction of the whales and elephants today

Increase in intelligence is claimed to be one of the signs of progress in evolution In vertebrates especially, there is a progressive series of forms showing greater and greater intelligence, ranging from fishes to man Accompanying and underlying this increase in intelligence, there has gone on in vertebrates a steady increase in the size, specialization, and compactness of the brain and its associated sense organs This steady trend is commonly spoken of by students of vertebrates as *cephalization* Is the final goal of evolution then the production of more and more intelligent organisms? If that were true, why should so much evolution be going on that seems to be moving in the opposite direction, resulting in the decephalization of many sedentary organisms and parasites?

You see it is difficult to discover any general or universal goal of evolution We do not even agree as to the direction of evolution, so we cannot be sure what is progress and what is regress Under these circumstances it may seem at first thought rather futile to discuss guiding factors at all Most of us however retain the firm conviction that evolutionary change has in it something of direction something of fitness, and something of progress though we may not always be able to demonstrate direction or fitness or progress in particular cases

Evolutionists, however have alway assumed that evolution is progressive that adaptation is a reality and that there have been definite evolutionary trends Believing in these phenomena they have tried to explain them The two classic attempts to explain progressive evolution are Darwin's theory of natural selection and Lamarck's theory of the inheritance of acquired characters These theories are to be critically discussed in chapters xxx and xxxi respectively

CHAPTER XXVIII

ADAPTATION IN NATURE

THE NATURE OF ADAPTATIONS

"The adaptation of every species of animal and plant to its environment," says Jordan and Kellogg[1] "is a matter of everyday observation So perfect is this adaptation in its details that its main facts tend to escape our notice The animal is fitted to the air it breathes, the water it drinks, the food it finds the climate it endures the region which it inhabits All its organs are fitted to its functions all its functions to its environment Organs and functions are alike spoken of in a half figurative way as concessions to environment And all structures and powers are in this sense concessions in another sense, adaptations As the loaf is fitted to the pan, or the river to its bed so is each species fitted to its surroundings If it were not so fitted it would not live But such fitness on the vital side leaves large room for variety in characters not essential to the life of the animal"

The authors quoted above appreciate what is perhaps the most significant fact about adaptations that the adaptations are to a large extent molded by the environment and therefore fit the environment So long as the environment remains uniform a given species will remain unchanged except for minor fluctuations and occasional mutations but if the environment changes sometimes even slightly the development of the individual responds in such a way as to give a radically different end product So we may conclude that a large part of the fitness of the organism to the environment is due to the fact that the development of each individual is molded by the environment so as to fit it Thus some at least of the apparent mystery of adaptations is dispelled

When we think of the fitness of the organism to the environment we take an entirely one sided view of the matter for if the organism fits the environment no less certainly must the environment fit the organism This idea of the fitness of the environment has been

[1] From D S Jordan and V L Kellogg *Evolution and Animal Life*

admirably discussed by Professor Lawrence J Henderson in a stimulating volume[1]

Henderson points out that the environment no less than organisms has had an evolution The particular environmental complex as it exists today is absolutely unique There is hardly an element of the effective environment that could be changed without causing the extinction of life or at least a transformation of it so profound that it might not be life at all as we know life Water for example, has a dozen unique properties that condition life Carbon dioxide could not be replaced by any other substance The properties of the ocean are so beautifully adjusted to life that we marvel at the exactness of its fitness Finally the chemical properties of carbon, hydrogen, and oxygen, the most abundant elements, are equally unique and unreplaceable In brief given the environment as it is life could not be other than it is The evolution of the environment and the evolution of organisms have gone hand in hand or perhaps we might better say hand in glove for this better expresses the idea of mutual fitness

Within the realm of the general environment as conceived by Henderson there are almost innumerable special environments due to particular combinations of the various environmental units Within the aquatic environment for example there are variations such a differences in salinity, varying from extreme saltness to almost total lack of salt there are inshore conditions and open sea conditions there are surface conditions and those at relatively great depths and there are great differences due to temperature Similarly on land there are surface conditions subterranean conditions arctic tropical conditions caves deserts forests plains, mountains and many others No two areas on land are precisely similar in all respects All of this makes for a corresponding multiplicity of animal and plant forms In the case of plants the action of the environment is remarkably direct for the plant cannot get away from a fixed environment If the environment undergoes material change, the plant s only response is a structural one For example, if plants that are accustomed to a relatively humid climate are grown in the desert they develop numerous xerophytic adaptations such as small leaves with greatly diminished transpiration surface a thick epidermis hairs or spines small stature, deep-root system and other similar protections against the inimical desert conditions Similarly plants accustomed to grow in relatively

[1] L. J Henderson *The Fitness of the Environment* 1913

dry soil if grown in soil that is covered over with water will produce aquatic leaves and roots and undergo appropriate changes in epidermis and loss of supporting tissues for plants that are buoyed up by water need little support

Animals on the other hand are for the most part not so intimately related to a local environment as are plants They are characteristically mobile creatures with varying capacities for wandering about and selecting the habitat that best suits them

'By virtue of being unlike or possessing different properties, says Shelford[1] ' the various animal species require different conditions for the best adjustment of their internal processes For example the carp lives in shallow and muddy ponds and rivers while the brook trout lives only in clear swift streams These two organisms are able to move about and find places to which they are suited The differences between them are clearly indicated by the differences in the habitats which they prefer

By observation and by experimentation it has been shown that animals select their habitats By this we do not mean that the animal reasons, but that selection results from regulating behavior The animal usually tries a number of situations as the result of *random movements*, and stays in the set of conditions in which its physiological processes are least interfered with This process is called selection by trial and error If animals are placed in situations where a number of conditions are equally available they will almost always be found living in or staying most of the time in one of the places The only reason to be assigned for this unequal or local distribution of the animals is that they are not in physiological equilibrium in all the places However, some animals move about so much that it is with some difficulty that we determine what their true habitats are

This idea of habitat preference and habitat selection is extremely important for a correct understanding of adaptation or the fitness of organisms to environments Much of the observed fitness may be due to the fact that an organism has chosen out of a wide range of environments the one that best suits it We cannot in such a case say that the environment has had a direct influence in shaping the organism any more than we could say that when a man tries on various shoes and finds a pair to fit he has been responsible for the fitness of the shoes

Many special adaptations may be explained through habitat choice. Thus animals such as the duckbill platypus the lung fishes,

[1] V E. Shelford, *Animal Communities in Temperate America* (1913)

and others whose teeth are replaced by bony or chitinous plates that are used for crushing the hard shells of molluscs and crustaceans, may not confidently be said to have developed these crushing appliances and to have abandoned the use of teeth in adaptation to a habit of feeding upon hard shelled prey, but rather it seems more likely that the loss of teeth and the development of crushers occurred through a degenerative process incident to racial senescence and that the possession of the crushing equipment enabled them to avail themselves of a new type of food formerly unavailable to them

The organic environment —In his admirable chapter entitled "The Web of Life," which we shall quote entire Professor Thomson has given us a vivid picture of vast systems of interdependencies that exist throughout the organic world No species no creature, lives to itself alone it is intimately tied up with a host of other creatures with interwoven destinies Thus one species of animal is adapted to live upon certain plants or other animals which in turn may be dependent upon still other animals or plants The elimination of one species may cause the elimination or the radical change of a dependent species We cannot afford ever to forget this great truth of the oneness of nature It is the keynote of life and of evolution

Adaptation due partly to functional activity —It is a commonplace which needs no special demonstration to say that organs improve through use and deteriorate through disuse Many organs, then which in the adult condition appear to us to be so admirably adapted to perform certain duties, must be thought of as having been gradually molded by functioning during the entire period of individual development If the motor nerve running to a limb bud of a growing embryo be severed at an early stage and no secondary nerve connection be established the limb will continue to grow up to a certain point, but in its paralyzed condition will be incapable of exercising its functions and will cease to develop A certain amount of development will therefore be seen to be independent of functioning but full development of functional efficiency is obtained only through functioning

"The relation between structure and function in an organism says Professor Child[1] " is similar in character to the relation between the river as an energetic process and its banks and channel From the moment that the river began to produce structural configurations in its environment the products of its activity accumulated in certain

[1] C. M Child "Regulatory Processes in Organisms *Jour Morph* Vol XXII (1911)

places and modified its flow It moulds its banks and bottom forming here a bar there an island here a bay there a point of land but still flowing on though its course its speed its depth the character of the substances which its carries in suspension or in solution all are altered built up by its own past activity According to this view structure is simply the resultant of the interaction of function and environment or of functional activity Though perhaps a little extreme for most of us this view is we believe essentially correct. We are prone to overemphasize structure in our discussions of adaptation and evolution and to lay too little stress upon the energy side of development Certainly no structure is ever formed without protoplasmic activity of a very definite sort and in this sense adaptations are to be thought of as the results of functioning Why then do we claim to be astonished at the effective way in which certain organs accomplish their functions when functioning has taught them their task?

TWO CATEGORIES OF ADAPTATIONS

There are according to E G Conklin two categories of adaptations (a) racial or inherited adaptations and (b) individual acquired or contingent adaptations. All of the direct molding effects of environment or of developmental functioning together with adaptative relations resulting from habitat selection or from learning and experience may well be classed as individual acquired or contingent adaptations As such they do not offer any particular problem to the evolutionist for they concern themselves with individuals not with races The adaptive condition is simply made over afresh in each generation and the only thing that seems to extend beyond the immediate individual or generation is a general plasticity or responsiveness of the specific protoplasm which enables it to adjust itself to special life conditions There is nothing mysterious or baffling about this situation for it involves merely a repetition of certain appropriate responses by each individual It is a problem of individual development not of racial development or evolution

Inherited Adaptations—There is however a large category of adaptations which appear in the organism as though in anticipation of the rôle they are to play some time in the future and not in response to any present need In this category are the eyes the lungs the vocal organs the taste buds and many other organs of the human fetus

Thus the eyes of the new born infant are essentially finished mechanisms before they ever function as organs of vision They cannot therefore have been molded for their visual function by functioning in a visual manner Of course they must have been functioning in some way, as all living protoplasm must function, but they cannot have functioned in a way that would in itself account for the fact that the eye is a very intricate optic mechanism Similarly, the human infant has good lungs and good vocal cords before it ever takes the first breath of air or gives the first cry Such adaptive structures as these are said to be *racial* or *inherited adaptations* Any theory of evolution worthy of the name must account for the origin and perpetuation of such inborn adaptations It was partly to explain the origin and perfection of adaptations such as these that Lamarck proposed his theory of the *inheritance of acquired characters* and Charles Darwin devised his theory of *natural selection* It is still unsettled as to which of these theories is the more adequate but the consensus of expert opinion favors Darwin s explanation

It would be impossible to give any comprehensive account of animal or of plant adaptations in the brief space of such a chapter as this Let it suffice to classify adaptations and to describe a few representative adaptations confining our attention to those which are obviously racial or inherited in character

ADAPTATIONS CLASSIFIED

Adaptations are variously classified by different authors and that of Jordan and Kellogg is as good as any (*a*) food securing (*b*) self defense (*c*) defense of young (*d*) rivalry (*e*) adjustment to surroundings

Some very common adaptations may belong to several of these categories at once Thus the sharp teeth and hooked claws of carnivorous mammals serve equally well for food securing, for self defense for defense of young and for rivalry Similarly the horns of deer and other ungulates are equally adapted for self defense defense of young and rivalry

There can be no especial advantage, in this connection in presenting a detailed review of adaptations of the sorts given in the foregoing classification therefore we shall confine our efforts to a description of a few typical adaptations about which the greatest controversy has raged

SOME SPECIAL ADAPTATIONS

The electric organ of the torpedo a widely distributed elasmobranch fish consists of a sort of honeycomb like structure on each side of the head This structure acts as a storage battery and is capable of storing up electricity of considerable voltage The animal is capable of giving a very distinct shock to an attacker and can thus defend itself quite effectively There is also an electric eel native to the waters of Paraguay and Brazil that is able to give severe shocks to bathers or to horses driven through the streams A type of catfish native to the river Nile has a similar electric equipment In all of these cases the storage battery is made up of modified voluntary muscles and is of considerable size

The mammary glands of mammals are skin glands usually with well-defined ducts leading to the surface and terminating in teats These glands are quite voluminous and serve admirably the purpose of feeding new born young until the latter are able to use the more varied food normal to the adult. In the lowest mammals the monotremes or egg laying mammals these glands are relatively poorly developed and diffuse, also they are known to be developed through a regional specialization of sweat glands In the true mammals or Eutheria the glands are modified sebaceous or oil glands and may be seen to develop from the same embryonic rudiments as the latter

The marsupial pouch of the kangaroo and its allies is a pocket like fold of the integument folded forward or backward over the region of the abdomen in which are located the mammary glands This pouch is used as a shelter for the tiny immature larval foetuses Hartmann has recently described a very striking piece of behavior in connection with the birth of young opossums The young are born in an exceedingly immature state and looking like tiny pink grubs They crawl under their own power by means of a swimming like motion through the hairs of the mother s abdomen till they reach the pouch This they enter unaided and each tiny larva finds for itself a slender tubular teat which it swallows and holds in place by a specially adapted hold fast mouth The young remains attached fixedly to this teat for some weeks feeding almost constantly on milk After a long interval the teat is released the mouth metamorphoses into the adult form and the young feeds only at intervals as do the young of other mammals This complex of adaptive structures and instincts is among the most remarkable in the annals of biology

The fetal membranes of higher mammals constitute one of the most efficient adaptive complexes known. Surrounding the embryo is a fluid filled sack (amnion) which furnishes an aquatic environment for the soft and delicate body, preventing harmful contacts and allowing ample free space for expansion. The placenta is a co-operative structure developed out of both fetal and maternal materials, that furnishes an excellent medium for nutritive and other metabolic exchanges between mother and fetus. Although there is no direct vascular connection between them the mother gives of her nutritive materials to the fetus and takes up from the fetus and eliminates its wastes. As an adaptation for carrying out an intricate set of physiological exchanges between two otherwise entirely separate individuals the placenta is unexcelled.

Nest making instincts in birds represent, on the behavior side adaptations of extraordinary perfection. Some nests are built with the greatest care and precision, others represent a relatively crude and slovenly performance. Some nests are made of twigs fibres, and mud others of mud alone still others are hollowed out in clay or sand banks and some are made in holes in the ground. In any case the type of nest is highly specific and due to a hereditary instinct, for birds receive no instruction in nest making.

Before bringing to a close this brief list of particularly noteworthy adaptations let us recall to mind the series of special adaptations listed as examples of the laws of adaptation such as aquatic, arboreal, cursorial flying burrowing ant eating and, especially, adaptations of deep-sea animals.

PARASITISM AND DEGENERATION

A vast number of animals and plants have given up the active search for food and have taken up the relatively easy habits of parasitism. In adaptation to this life certain structures have developed and many of the characters found in independent, free-roving creatures have disappeared or become reduced to mere vestiges. Thus the more completely dependent or parasitic an animal becomes the more completely does it lose its organs of locomotion and its sense organs such as eyes, auditory organs tentacles etc. Some animals are free living when young or in the larval condition and only settle down to a parasitic life when near the end of the life-cycle other animals are parasitic only when young or larval and become independent in the adult condition still others are parasitic throughout the entire life-cycle and pass from host to host without any interval of independent life. Some of these complete parasites pass one phase of the life-cycle on one species of host and the remainder on another

species of host. Thus the liver fluke in the adult condition lives in the gall bladder of the sheep, while the early larvae live within the body cavities of a species of land snail. The transfer from host to host in this case must be a procedure involving many chances of failure to a very few chances of success and in adaptation to these vicissitudes the number of eggs and larvae produced by a single adult individual runs up into the millions.

The classic case of extreme parasitic degeneration is that of *Sacculina*. The young larva of *Sacculina* is a typical entomostracan crustacean larva which swims about and leads a free life for a time but soon attaches itself by means of its antennae to a hair pit of a crab, a small hole in the latter's armor. The internal tissues of the larva then undergo degenerative processes and are reduced to an almost fluid mass of embryonic cells which flow through the hair pore of the crab and into the latter's lymph spaces. The small mass of cells then rounds up and is carried about with the circulation of the crab's blood until it comes to a favorable place of lodgment, usually the wall of the intestine just back of the stomach. Here it flattens out and sends rootlike branches almost all over the crab's body, like a malignant tumor in its invasion of foreign tissues. The unbranched part of the parasite is little more than a sac of reproductive organs, and these produce eggs and sperms which unite to produce larvae. By this time the host is killed and with the decay of its body the larvae escape into the sea water ready for a brief period of free life before attacking another host.

Almost every group of animals and most of the groups of plants have their parasitic representatives and every degree of parasitism and the accompanying degenerative changes are to be found. Of course it is an open question whether parasitism causes degeneration or whether degenerating creatures take refuge in parasitism, but in either case the adaptive features of the situation are obvious.

Commensalism.—If parasitism be defined as an association between two organisms in which one (the parasite) lives at the expense of and to the detriment of the other (the host), commensalism may be defined as an association in which the two organisms exist in close association without any positive detriment to either. In some cases the claim is made that the association is mutually beneficial, but as a rule the relation is relatively one-sided.

An interesting example of commensalism is that of the sea cucumber and the little fish *Fierasfer*. This strange little animal inhabits

the rectum of the sea cucumber and may be seen to lie with only its head out From this shelter it darts forth to capture its prey which done it returns to its shelter Curiously enough the vent of the little fish is situated just back of its mouth so that its wastes may be voided when in its usual position There can be no advantage to the sea cucumber in such an arrangement though no particular harm is done Another case of this sort is that of several species of Remora which attach themselves by a large diskoid adaptation on top of the head to various fish such as sharks barracudas etc

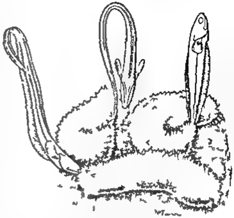

FIG 78—*Fierasfer acus* penetrating the anal openings of holothurians ⅔ natural size (*From Boulenger after Emery*)

The sucking disk is a modified dorsal fin The remora merely gains free transportation to more favorable feeding grounds When the desired food is sighted the passenger leaves its conveyance temporarily but returns by a sudden swift dash and resumes its hold The shark gets nothing except perhaps the sense of companionship and is also undoubtedly somewhat hindered in its locomotion

Some of the most remarkable cases of commensalism are found in connection with elaborate colonies of ants In some cases two species of ants live together in the relationship of masters and slaves The master species is unable to perform any of the ordinary duties of the colony such as securing food, taking care of young etc In extreme cases the masters are only soldiers, specialized for fighting and marauding and cannot even feed themselves unaided The slave species would be able to carry on to some extent if not captured but thrives exceptionally well under the protection of the soldier species There are among ants many varieties of commensal relationship less extreme than this, but this will serve as a typical case

Communal life —Among the higher insects and higher vertebrates especially among the ants and bees we find a very elaborate social life In ants for example the typical colony consists of a queen (the only fertile female in the colony) several males (mates of the queen),

ordinary workers (sterile females of the first type) soldiers (sterile females of the second type) and sometimes officers (especially large and powerful sterile females that seem to direct the line of march in legionary ants) All of these casts are produced from the eggs of one female and are the result of various special diets permitted the larvae by the workers Among bees similarly, there is one queen a number of drones (males) and the sterile female workers who perform the functions of nursing the larvae cleaning up the hive collecting pollen and nectar, and making honey and wax Detailed accounts of the lives of bees have been given by various authors notably by Maeterlinck in his *Life of the Bee*

ADAPTATIONS OF DEEP SEA ANIMALS AND OF CAVE ANIMALS

One of the weirdest environments the world affords is the bottom of the sea at great depths There it is dark and cold and almost devoid of oxygen while the pressure is almost unbelievably high Yet in these vast and forbidding abysses there dwell in apparent comfort representatives of most of the animal phyla Fishes of many sorts crabs mollusks, worms and many other forms thrive and multiply in this seemingly cheerless environment We do not at all understand the nature of the adaptive mechanism that enables these animals to withstand with their frail bodies the steel crushing pressures that prevail at all such depths We do know however, how some of the deficiencies of the environment are made good by these denizens of the deep Thus many abysmal forms produce their own light by means of phosphorescent organs placed at advantageous points of their bodies Not only fishes of the depths but some mollusks possess forms of artificial lighting equipment One species of cephalopod (related to the octopus) is described by Wiesmann as bordered with twenty large phosphorescent lanterns that present the aspect of a display of variegated gems colored ultramarine ruby red sky blue and silvery white

Equally highly adapted to life in a world of darkness the monotony of which is broken only by the occasional spots of light emanating from the various living lanterns just referred to are the strange eyes of some of the abysmal fishes Sometimes these eyes are enormously large and thus adapted to bring to the perception of the animal the weak light of the depths or again they may be modified still further in a strikingly peculiar manner each being drawn out into a cylinder and projecting from the side of the head like a telescope Such eyes are in fact not telescopes though they are called telescope eyes' but are merely adaptations for concentrating the lights of low intensity

and making the environment visible Could man view the sea bottom through some of these instruments, he would doubtless add something very novel and weird to his scenic repertoire

Other creatures of the darkness live strange lives in caves such as the Mammoth Cave of Kentucky Most cave dwellers are blind or nearly so and usually have a pale and ghostlike appearance because of their lack of pigment All grades of defective eyes are found, ranging from those that are merely somewhat smaller than normal to those that remain deeply imbedded in the head in a relatively undifferentiated state It goes without saying that such animals are better adapted to life in caves than they would be outside One pressing problem of biology is How did the cave animals become blind? Did they wander into the caves as normal animals and become blind because their eyes were disused or did they become blind outside through no fault of their own, as the result of a mutation and by chance find safety in an underground stream or a cave? The first explanation is Lamarckian the second Darwinian

COLOR AND PATTERN IN ANIMALS

The phenomena of color in both animals and plants, says Metcalf[1] are among the most remarkable and interesting in the whole realm of nature It is not so much the way in which the color is produced whether by pigments or by refraction that interests us in this connection as it is the uses to which colors are put Let us first refer to the colors of animals

'According to the uses to which colors in animals are put, we may classify them for purposes of description as follows

"Indifferent coloration not useful so far as we can judge
Colors of direct physiological value
Protective coloration and resemblances,
Aggressive coloration and resemblances,
Alluring coloration and resemblances,
Warning coloration
Immunity coloration
Mimetic coloration and resemblances,
A Protective
B Aggressive
Signals and recognition marks,
Confusing coloration
Sexual coloration"

[1] M M Metcalf *Organic Evolution* (1911)

Much has been written about these various categories of animal coloration nearly all of which assumes some special adaptive value for each type of color or pattern

The above classification is typical of the older views as to animal coloration in that it recognizes no colors as merely incidental by products of metabolism but assumes that all colors are valuable as adaptations Modern critics are inclined to consider that at least many colors are to be explained as the result of the fact that certain chemical materials are formed in the elaboration of tissues and in the physiological processes that must go on in these tissues which because of their light absorptive properties appear to our eyes as colored The color may chance to enhance the protective resemblance of the animal or it may make it more conspicuous than it should be in either case it may have an incidental value But colors may come and colors may go irrespective of adaptive value for many colors are so placed in the organism that they can never be visible and color is only in the seeing While we have no intention of denying the adaptive value of animal colors it seems wise to get away from the extreme anthropomorphic interpretation of these colors for some of the categories of coloration listed in the previous paragraph are largely if not wholly anthropomorphic It has been the habit of students of coloration to assume that insects birds lizards and other animals see colors and patterns as man sees them that what is attractive to man must also be attractive to the lower animals that what is confusing to man would also be confusing to a lizard or an owl Experiments with lizards which are supposed to be chief among the factors giving adaptive significance to insect coloration have shown that the lizard apparently takes no notice of colors at least when they are at rest but will jump at any moving object of about the right size

Modern students are inclined to think that many of the minor categories of animal coloration listed above are at best of very questionable significance and that practically all categories simmer down to one *obliterative coloration or camouflage*

All naturalists says G H Thayer perceive the wonderful perfection of the twig mimicry by an inchworm or of bark by a moth or of a dead leaf by the Kallima butterfly It is now apparent that almost equally marvelous concealment-devices in one shape or another are general throughout the animal kingdom *the most gorgeous*

G H. Thayer *Concealing Coloration in the Animal Kingdom* The Macmillan Company 1918

costumes being in their own way climaxes of obliterative coloration scarcely surpassed even by moths or by inchworms

This discovery that patterns and utmost contrasts of color (not to speak of *appendages*) on animals make *wholly* for their 'obliteration is a fatal blow to the various theories that these patterns exist *mainly* as nuptial dress, warning colors, mimicry devices (i e mimicry of one species by another), etc, since these are all attempts to explain an entirely false conception that such patterns make their wearers *conspicuous*. So immeasurably great in the case of most animals, must be the value of inconspicuousness that such devices as achieve this to the utmost imaginable degree upon almost every living creature demand no further reason for being (although doubtless serving countless minor purposes) Apparently not one 'mimicry mark, nor one 'warning color' or banner mark nor one of Gadow's light and shadow begotten marks nor any sexually selected color, exists anywhere in the world where there is not every reason to believe it is the very best conceivable device for the *concealment* of its wearer either throughout the main part of this wearer's life or under certain peculiarly important circumstances The so-called 'nuptial costumes of animals are demonstrably an increase of such potency of obliterative coloration as belongs to all gorgeously varied costumes, *and this at the very period when concealment is most needed*

Thayer believes 'that the colors, patterns and appendages of animals are the most perfect imaginable effacers under the very circumstances wherein such effacement would most serve the wearer Many animals when observed in a museum show case or in a menagerie, appear to us to be most conspicuous but the elements that lend conspicuousness in the artificial environment may be the very ones that tend to efface the wearer when in his native haunts The most brilliant birds such as mandarin ducks birds of paradise flamingoes peacocks parrots, etc, are shown to be almost invisible in their natural surroundings

The schemes for producing obliterative protection are much the same as those made use of during the recent war The simplest scheme of all is that of having the same color and pattern as the background Thus many green insects amphibia, reptiles, birds and a few mammals that live in trees smaller plants or grass, are colored green Many desert animals are sand colored Many marine animals living near the surface are transparent or nearly so Another scheme is known as *counter shading* according to which most animals with little variety

of color are concealed by having the upper surfaces dark the lower s faces light and a blending of one into the other on the sides Nea all birds of the open such as sea birds and soaring birds use method of concealment The same is true for fishes that live near surface and for many mammals that are likely to be seen agains sky line Actual demonstrations have shown that this method concealment is highly effective, no matter from what point of view animal may be seen A third scheme is one that was used most ef tively during the war in concealing battleships, heavy artillery other large objects namely, destroying the continuity of outline using large irregular patches of contrasting or light and dark col In this way a broken irregular patchwork of color takes the place a coherent regular contour It is probably in this way that many the most brilliant coral reef fishes attain concealment. Instead of fish as a whole being the center of vision, the bright patches stand against the dark and these fail to give any picture likely to be in preted as a fish either by enemies or by prey Professor Reighard terpreted the brilliant patterns of reef fishes as examples of immun coloration, the idea being that these fishes were so safe from att and so little in need of concealment from prey that they simply w the limit in color display, unchecked by natural selection Long has recently shown that the patterns and colors of such fishes are reality obliterative and if this be true there is no need of introduc the idea of immunity coloration

In view of the above considerations, it now seems likely that ess tially all types of animal coloration that have any adaptive value at —and by no means all have any demonstrable adaptive significanc may be classed under the general head of concealing coloration, an thus be so it greatly simplifies the problem of the evolutionist M of the controversy as to the efficacy of natural selection has been wa about some of the questionable categories of animal coloration s as warning coloration mimicry confusing coloration 'sex coloration If all of these turn out to be merely phases of conc ment coloration their origin could be explained as readily as that any other adaptive character of definite selective value

The Case of Kallima—With this general introduction to the s ject of animal coloration it does not seem necessary to list example all the categories of color mentioned Let us close the discussion w what appears to be the classic instance in biological literature of per protective resemblance that of the dead leaf butterfly *Kall* (Fig 79)

"Its wings says Herbert, 'when upturned represent on their underside a perfect copy of a leaf with a midrib and a regular succession of side veinings Differently colored spots on the wing imitate patches of decay and mildew, while the prolonged tail of the hind wing which touches the stem in the sitting posture of the butterfly,

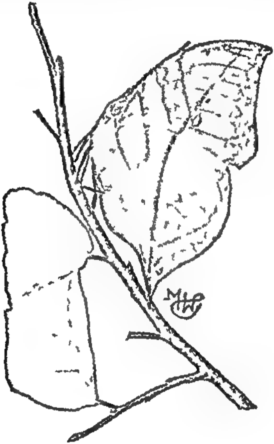

FIG 70—*Kallima* the dead leaf butterfly (*From Jordan and Kellogg*)

makes it appear as though the leaf was directly growing out of the stem It is only when at rest upon the stem of a tree that the resemblance to a leaf would be effective, for it is only the under surfaces of the wings that are protectively colored The upper surfaces of the wings are brightly colored and would supposedly be quite conspicuous when the insect is in flight These insects, says Metcalf "are very noticeable when in flight but when they light and close the wings their

sudden disappearance is most startling and confusing greatly increasing the difficulty of observing their resting place' According to this idea of 'confusing coloration, a butterfly is supposed to mystify or confuse its enemies by first attracting their attention and then suddenly becoming invisible One is reminded of the prestidigitator of his favorite remark 'Now you see it and now you don t But why attract attention in the first place when continued inconspicuousness would be much less risky? The best answer to this question is to use Thayer s interpretation namely that what looks like a conspicuous coloration when observed in the stationary insect held against an alien background is probably almost invisible when the animal is moving its wings and flying through the air in the bright sunlight

The case of *Kallima* is probably more or less typical of the somewhat uncritical tendency on the part of naturalists to invent adaptive explanations for every striking color or pattern seen among animals Let us examine the situation a little further Much has been said about the minute details of resemblance to a dead and decaying leaf on the part of this butterfly yet if its habits are at all like those of other members of its order, it is hardly likely that its most active period would coincide with that in which the leaves of trees would be decayed and mildewed or even brown Butterflies are active when flowers whose nectar forms their chief food, are numerous and are usually in their pupa cases when the leaves have died on the trees It has also been stated by critical observers that *Kallimas* do not frequently light on trees whose leaves are very similar in shape to the folded wings of a butterfly Furthermore there are many kinds of butterflies that are more or less like leaves in fact it would be difficult for a butterfly not to look somewhat like a leaf since the wings are shaped like leaves Again many species of butterflies have the swallowtails on the lower wings without in other ways much resembling a leaf others have spots that might be interpreted as resembling decay and mildew without in other ways being more than in general leaflike and there are many other species that show all degrees of leaf resemblance, some very imperfect and others almost as perfect as that of *Kallima* yet they all seem to be essentially successful in the life-struggle in spite of their less perfect protective resemblance

Alleged cases of mimicry have failed also to meet critical examination When a poisonous butterfly is mimicked by an edible species several conditions must be met in order that the deception be effective The model and the mimic must both occupy the same range

have the same period of activity and the same general habits The model must be much more numerous than the mimic Unfortunately for the proponents of mimicry, it has sometimes been found that several of these requirements are lacking Attempts to explain away the discrepancies have been far from satisfactory

All these considerations should make us cautious about reading into the colors and patterns of animals too many adaptive details It is more than likely that the majority, if not all, of these apparently marvelously exact instances of imitative resemblance would turn out when critically examined to be no more nor less adaptive in special ways than is *Kallima* and the mimics

One lesson that the naturalist may well learn from the present discussion is this There is enough in the way of adaptations for the evolutionist to explain without burdening him with hypothetical or interpretative adaptations First find and prove your adaptation then try to explain it Don t explain it fir t and then find out later that it was not so much of an adaptation after all

OSBORN S LAWS OF ADAPTATION

Adaptations have been variously cla sified by different writers Perhaps the most significant classification is that of Osborn which is based on their supposed evolutionary origin According to this writer and others there are two categories of adaptations to environ mental conditions the first has to do with the tendency of unrelated species to assume similar structures under similar environmental conditions the second has to do with the tendency of related species to assume different adaptive structures under different environmental conditions In both categories the environment appears to be the determining factor

(1) A good example of the first category which illustrates what Osborn calls "the law of convergence or parallelism of form," is seen in the tendency of *many aquatic types of vertebrates to assume* the fishlike form As is well shown in Fig 80 the shark (a fish) the ichthyosaur (an extinct aquatic reptile) and the porpoise (a marine mammal) all possess the same fusiform body best adapted for speed under water the same types of locomotor structures consisting of the great propeller fin (caudal fin) and the steering and balancing fins the dorsal fins and paired fins Apart from these superficial adapta tions for swift locomotion in the water the three types are profoundly different The shark breathes with gills the reptile and mammal with lungs the fish and reptile are cold blooded the

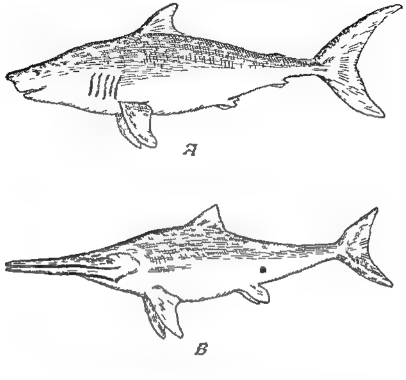

FIG 80 — Three aquatic types of vertebrates to illustrate convergent adaptation of three wholly unrelated forms of marine life All three show the fusiform body median and paired fins though the skeletal structures are radically different A shark (Pisces) B ichthyosaur (Reptilia) C porpoise (Mammalia) (*From Newman after Osborn*)

mammal warm blooded The internal anatomy of the three differs fundamentally in every detail

A list of other types of convergence will more adequately illustrate the law

Flying and parachuting animals occur among nearly all vertebrate and some invertebrate classes Planes of some sort are found for supporting the body in the air The plane is made in various ways in different groups but functions much the same in all of them

Running animals of various classes have long legs and a tendency to stand on the toes There is also in several unrelated groups the tendency to reduce the number of toes the culmination of which is seen in the one toed horses

Climbing animals are all provided with clinging appendages of some sort including such structures as hooked claws prehensile fingers or tail, suction pads on the feet and other similar adaptations

Burrowing animals have as a rule extra heavy shoulder girdle and strong fore limbs with heavy gouging claws Many of them also are blind or nearly so as befits life in dark underground passages

Desert-dwelling animals as a rule are provided with heavy scales spines or armor to prevent excessive loss of moisture and as a protection against spiny plants They also usually have burrowing habits enabling them to escape the extremes of heat and cold

Cave animals are usually blind or nearly so and are relatively pale in color sometimes without any pigmentation

Deep-sea animals of many sorts have phosphorescent organs by means of which they either attract their prey or find their way about the dark sea floor Some of these organs called "lanterns" can be used as searchlights The eyes of deep-sea fish are either enormously large or are telescope eyes adapted for sensing light of low intensities

Ant eating animals, belonging to several distinct groups are heavily armored against the attacks of ants have strong claws for digging up ant galleries, have long snouts or beaks with a long sticky tongue for capturing ants and an arrangement of the glottis to prevent ants from crawling into the lungs

2 There are almost innumerable examples of the law of divergence of form, which is called also the law of adaptive radiation Almost every successful class or order of vertebrate animals for example has members that have adjusted themselves to all of the main modes of living Thus among lizards, for example, there are primitive

running forms that prefer the surface life and swift motion subterranean burrowing types that sometimes are limbless like snakes and are blind many arboreal or climbing types a few volant or flying types a few ant eating types and several more or less completely aquatic types Each of these types has the customary adaptations for its own mode of life

We see then that whether divergent structures are molded into a semblance of similarity to fit a definite environment or whether similar structures are modified in diverse ways to fit various divergent environments the adaptation is related very definitely to the environment and to the functional life of the organism No wonder then, that so many biologists consider that the environment has been a molding force in the evolution of adaptations

General considerations —Adaptations are characteristic of all living organisms and must be accounted for by any evolutionary theory that is to be acceptable Any theory that claims to account for new species but does not account for adaptations is at best only a partial explanation All of the phenomena which have been briefly mentioned in this chapter together with the more intricate phases of general adaptiveness involved in the idea of the web of life are part of the background of Darwinism and were in the mind of Darwin when he thought out the great generalization called natural selection The web of life idea has been admirably presented by Professor Thomson Scotland s most skilful and prolific biological writer The present writer feels that no student of evolution should miss the opportunity of getting into the spirit of Darwinism with this distinguished author and to make this desideratum easily attainable the chapter is quoted unchanged as part of the general text and immediately follows this discussion

CHAPTER XXIX

THE WEB OF LIFE[1]

J ARTHUR THOMSON

Naturalists in the true sense who study the life of living creatures in nature have always been distinguished by a keen perception of the interrelations of things Whether we take Gilbert White as representing the old school or W H Hudson as representing the new, we get from their observations the same impression of nature as a vibrating system most surely and subtly interconnected But it seems just to say that no naturalist before or since has come near Darwin in his realisation of the web of life, in his clear vision and picture of the vast system of linkages that penetrates throughout the animated world

Correlation of organisms as well as correlation of organs —In thinking of a living body we are accustomed to the idea of the correlation of organs It is of the very nature of an organism that there should be mutual dependence among its parts The organs are all partners in the business of life and if one member changes others also are affected This is especially true of certain organs that have developed and evolved together and are knit by close physiological bonds We know in health how nerve and muscle brain and sense organs heart and lungs are closely bound together in the bundle of life We know in disease that a change in one organ often affect another and the fact remains though the nexus is sometimes mysterious The state of our liver may give colour to our whole intellectual firmament, and a slight ocular derangement may warp a wise man's philosophy The far reaching importance of a little organ like the thyroid gland beside the larynx is well known, our intellectual as well as our bodily health depends on its soundness Now, just as there is a correlation of organs within the body so there is a correlation of organisms in that system of things which we call Nature In both cases we are here using the word correlation in its deeper sense—

[1] From J A Thomson *Darwinism and Human Life* (copyright 1900) Used by special permission of the publishers Henry Holt & Company

that the various parts are more than mutually dependent that they are in some measure co-ordinated making larger systems workable

What the metaphor of "the web of life ' suggests —We may use the metaphor web of life in two ways On the one hand Nature has a woven pattern which science seeks to read each science following the threads of a particular colour There is a warp and woof in this web which to the zoologist usually appear as hunger and love ' There is a changing pattern in the web becoming more complex as the ages pass and *this is evolution* But the essential idea of a web is that of interlinking and ramifying We can never tell where a thread will lead to If one be pulled out many are loosened This is true of Nature through and through

The phrase ' web of life suggests another picture—the web of a spider—often an intricate system with part delicately bound to part so that the whole system is made one The quivering fly entangled in a corner betrays itself throughout the web often it is felt rather than seen by the lurking spinner So in the substantial fabric of the world part is bound to part In wind and weather or in the business of our life we are daily made aware of results whose first conditions are very remote and chains of influence not difficult to demonstrate link man to beast and flower to insect The more we know of our surroundings the more we realise that nature is a vast system of link ages that isolation is impossible

Dependence of living creatures on their surroundings —We do not know what life in principle is but we may describe living as action and reaction between organisms and their environment This is the fundamental relation—the dependence of living creatures on appropriate surroundings and the primary illustrations of linkages must be found here The living creatures are real, just in the same sense as the surroundings are real but it is plain that we cannot abstract the living creatures from their surroundings When we try to do this they die—even in our thought of them and our biology is only necrology Huxley compared a living creature to a whirlpool in a river it is always changing yet always apparently the same matter and energy stream in and stream out the whirlpool has an individuality and a certain unity *yet it is wholly dependent upon the surrounding currents* One may push the whirlpool metaphor too far so as to give a false simplicity to the facts for when vital whirlpools began to be there also emerged what cannot be discerned in crystal or dewdrop—the will to live a capacity of persistent experience and the power of giving rise to

other lives To ignore this is to attempt a falsely simple natural history But what Huxley s metaphor of the whirlpool does vividly express is the dependence of living creatures on their surroundings We cannot understand either the whirlpool or the trout apart from the stream

When we think out this fundamental dependence upon surroundings we see for instance that all our supplies of energy, all our powers of every kind—with our own hands, or by the use of animals or by means of machinery—are traceable to the sun Or again, it is easy to show that our society depends fundamentally not on gold but on iron We depend for food on plants and animals and through these animals on plants ultimately the plants feed upon air water, and salts, which, with the aid of the energy of the sunlight, they build up into complex organic compounds, they cannot do this unless the sun shines through a screen of green pigment called chlorophyll there cannot be chlorophyll without iron, *therefore* our whole social framework is founded on *iron*

Nutritive chains —Plants feed on their inanimate environment in a direct way that is impossible to animals so we pass insensibly from dependence on surroundings to those *nutritive chains* which bind living creatures together in long series often quaintly suggestive of The House That Jack Built and similar old rhymes We have ceased to wonder at the circulation of the blood in our body have we begun to wonder enough at the ceaseless circulation of matter in the system of nature? As Heraclitus said πάντα ρεῖ all things are in flux The rain falls the springs are fed the streams are filled and flow to the sea the mist rises from the deep and the clouds are formed which break again on the mountain side The plant captures air water and salts and with the sun s aid, builds them up by vital alchemy into the bread of life incorporating this into itself The animal eats the plant and a new incarnation begins *All flesh is grass* The animal becomes part of another animal, and the reincarnation continues The silver cord of the bundle of life is loosed, and earth returns to earth The microbes of decay break down the dead, and there is a return to air and water and salts We may be sure that nothing real is ever lost we are sure that all things flow Penelope like Nature is continually unravelling her web and making a fresh start

Nexus between mud and clear thinking —To keep a famous inland fish pond from giving out some boxes of mud and manure were placed at the sides Bacteria—the minions of all putrefaction—

worked in the mud and manure making food for minute Infusorians which multiply so rapidly that there may be a million from one in a week's time A cataract of Infusorians overflowed from box to pond, and the water fleas and other small fry gathered at the foot of the fall and multiplied exceedingly Thus the fishes were fed and, as fish flesh is said to be good for the brain we can trace a nexus from mud to clear thinking What was in the mud became part of the Infusorian which became part of the Crustacean, which became part of the fish, which became part of the man And it is thus that the world goes round

Correlation between catches of mackerel and amount of spring sunlight—A curious and most interesting correlation has been discovered by Dr E J Allen between catches of mackerel and the amount of sunlight The more sunshine in May the more mackerel at Billingsgate How does this work out? Mr G E Bullen shows that "for the years 1903–1907 there appears to be a correlation between the number of mackerel taken during May and the amount of Copepod plankton upon which the mackerel feed taken in the neighborhood of the fishing grounds during the same month Mr W J Dakin shows that the food of Copepods consists largely of the vegetable organisms of the plankton, such as diatoms and of Infusoria like organisms called Peridinidae But the production of this microscopic plankton the "stock of the seasoup depends partly on the composition of the sea water partly on the tempera ture and partly on the amount of light available There seems to be no correlation between the surface temperature and the abundance of mackerel but Dr Allen has shown a correspondence between sunshine and the catches Thus we see that if all flesh is grass then in the same sense all fish is diatom

Nutritive chains in the deep sea—If we pass from the sunlit open sea to the floor of the deep sea—that strange dark cold silent, plantless world—we find carnivorous animal preying upon carnivorous animal through long series—fish feeds on fish, fish on Crustacean Crustacean on worm worm on still smaller fry, and all ultimately depend on the basal food supply—the ceaseless shower of moribund atomies sinking from the surface waters many miles it may be over head like the snowflakes on a quiet winter day

Dependence of one organism on another for the continuance of the species—Passing from nutritive chains[1] we may select a few illustrations of the dependence of one creature upon another for the

continuance of its kind The crowning instances are to be found in interrelations between plants and animals which secure cross fertilisation and the distribution of seeds To both of these Darwin devoted much attention, and they were always favourite subjects with him

Everyone knows that flowering plants and flower visiting insects have grown up throughout long ages together in alternate influence and mutual perfecting They are now fitted to one another as hand to glove The insects visit the flowers for food in so doing they carry the fertilising golden dust from blossom to blossom, so that the possible seeds become real seeds

In 1793 a Berlin naturalist Christian Konrad Sprengel, like Darwin in his perception of the web of life, published a pioneer book entitled *The Secret of Nature Discovered in the Structure and Fertilization of Flowers*, in which he showed that most flowers have nectar which insects enjoy, that by the insects visits pollination is secured, that there is no detail of the flower without its meaning—the colour is a flag to attract the insect s eye conspicuous spots are honey guides to the explorers there are arrangements for keeping the pollen dry and for dusting it on the insects, and so on If Sprengel had only discovered the utility of the cross fertilisation, which Darwin proved experimentally his work could hardly have been overlooked for nearly seventy years In 1841 it came into Darwin's hands, and impressed him as being ' full of truth," although "with some little nonsense ' In Darwin's work Sprengel had his long delayed reward

Darwin s instance of the connection between cats and clover — One of Darwin s instances of the web of life—given in connection with the pollination of flowers—has become familiar all over the world It should never become trite to us and it should never be regarded as more than a particularly clear illustration of a general fact "Plants and animals remote in the scale of nature, are bound together by a web of complex relations I have found from experiments, that humble bees are almost indispensable to the fertilisation of the heart s ease (*Viola tricolor*) for other bees do not visit this flower I have also found that the visits of bees are necessary for the fertilisation of some kinds of clover—thus 100 heads of red clover (*Trifolium pratense*) produced 27 000 seeds but the same number of protected heads produced not a single seed Humble bees alone visit red clover as other bees cannot reach the nectar Hence we may infer as highly probable that if the whole genus of humble bees became extinct or very rare in England, the heart's-ease and red clover would become

very rare or wholly disappear We know that the red clover imported to New Zealand did not bear fertile seeds until humble bees were also imported ' The number of humble bees in any district depends in a great measure on the number of field mice which destroy their combs and nests, and Colonel Newman who has long attended to the habits of humble-bees believes that more than two-thirds of them are thus destroyed all over England Now the number of mice is largely dependent as everyone knows on the number of cats and Colonel Newman says 'Near villages and small towns I have found the nests of humble bees more numerous than elsewhere which I attribute to the number of cats that destroy the mice Thus we may say, with Darwin that next year s crop of purple clover is influenced by the number of humble-bees in the district which varies with the number of field mice that is to say with the abundance of cats!

Scattering of seeds—It is a fascinating chapter of natural history which tells us how cross-pollination is effected—here by a bee and there by a butterfly, occasionally by a long billed humming bird beautifully poised before the flower with almost invisibly rapid vibrations of its wings and occasionally by a slowly moving snail of epicure appetite But not less important is the part played by animals in the scattering of seeds and here again Darwin gives us the classic case of fourscore seeds germinating out of a ball of mud from a bird s foot From one instance you may learn all and see that much of Darwin s work has been an eloquent commentary on that memorable saying about the sparrow that falls to the ground Such a simple event literally sends a throb through surrounding nature we can follow its effects a few steps just as we follow for a few yards the ripples made when we throw a stone into a still lake in either case can we doubt that the spreading influences are real though they pass beyond our ken?

Interrelations between fresh-water mussels and fishes—As a striking illustration of the inter linking of different forms of life we may take the case of the fresh water mussels and their larvae The fertilised eggs develop in the outer gill plate of the mother mussel and minute bivalve larvae called *Glochidia* are formed. The mussel keeps these within the cradle until a fresh water fish—such as the minnow—comes into the vicinity and then she sets them free In a way that we do not understand, the simple constitution of the larvae is tuned to respond to the presence of minnows and the like and with snapping valves they manage to fix themselves to their host. After a short

period of temporary parasitism, at the end of which there is a meta morphosis they drop off from the fish into the mud, often far from their birth place This is curious enough, but the idea of linkages becomes incandescent in the mind when we note that just as the fresh water mussel has young temporarily parasitic on fishes, so a fresh water fish the bitterling (*Rhodeus amarus*), has its young temporarily parasitic in the gills of the mussel

Life histories of parasites —When we pass to parasites in a stricter sense we find the most extraordinary interconnections the most widely separated animals often sharing a parasite between them Liver rot which has repeatedly killed a million sheep in a year in Britain alone, is due to a parasite which passes from sheep to water from water to water snail, from water snail to grass, from grass to sheep The tapeworm of the cat has its bladder worm stage in the mouse, the sturdie worm of the sheep s brain has its tape worm stage in the dog, and similar relations hold for hundreds of species The troublesome threadworm of human blood (*Filaria sanguinis hominis*) is transferred from man to man by the mosquito and the guinea worm which was probably the fiery serpent that vexed the Israelites in the desert which passes into man in drinking water, spends its youth in a minute water flea, called by the giant s name of Cyclops The importance of tse tse flies in transmitting the minute animals which cause sleeping sickness and allied diseases is known to all We have spoken of the connection between cats and clover, and there is a not less striking connection between cats and plague For it seems to have been shown in India that the more cats the fewer rats and the fewer rats the fewer rat fleas which are the agents in passing the plague-germs to man

Far reaching influence of certain animals, earthworms —We realise the idea of the web of life in another way when we consider the far reaching influence of particular kinds of activity the best instance being the work of earthworms In 1777 Gilbert White got at the very root of the matter ' The most insignificant insects and reptiles are of much more consequence and have more influence in the economy of nature than the incurious are aware of Earthworms, though in appearance a small and despicable link in the chain of nature yet, if lost, would make a lamentable chasm Worms seem to be the great promoters of vegetation, which would proceed but lamely with out them by boring perforating and loosening the soil, and rendering it pervious to rains and the fibres of plants, by drawing straws and

stalks of leaves and twigs into it and most of all by throwing up such infinite numbers of lumps of earth called worm casts which being their excrement is a fine manure for grain and grass Worms probably provide new soil for hills and slopes where the rain washes the earth away and they affect slopes probably to avoid being flooded

The earth without worms would soon become cold hard bound, and void of fermentation, and consequently sterile These hints we think proper to throw out, in order to set the inquisitive and discerning at work A good monograph of worms would afford much entertainment and information at the same time and would open a large and new field in natural history

The monograph that Gilbert White wished for in 1777 was published by Darwin in 1881, the year before he died—" the completion he said, " of a short paper read before the Geological Society more than forty years ago With his characteristic thoroughness and patience he worked out the part that earthworms have played in the history of the earth and proved that they deserve to be called the most useful animals By their burrowing they loosen the earth making way for the plant rootlets and the raindrops by bruising the soil in their gizzards they reduce the particles to more useful powdery form by burying the surface with castings brought up from beneath they have been for untold ages ploughers before the plough and by burying leaves they have made a great part of the vegetable mould over the whole earth. In illustration of the last point we may notice that we recently found thirteen midribs of the leaves of the rowan or mountain ash radiating round one hole like the spokes of a wheel, the withering leaflets had been carried down and two were sticking up at the mouth of the burrow that meant 91 leaflets to one hole Darwin showed that there often are 50 000 (and there may be 500 000) earthworms in an acre that they often pass ten tons of soil per acre per annum through their bodies and that they often cover the surface at the rate of three inches in fifteen years Though our British worms only pass out about 20 oz of earth in a year the weights thrown up in a year on two separate square yards which Darwin watched were respectively 6 75 lb and 8 387 lb which correspond to 14½ and 18 tons per acre per annum

We follow the work further and it becomes evident that the constant exposure of the soil bacteria on the surface is bound to be important, on the one hand in allowing them to be scattered by wind and rain on the other in exposing them to the beneficent action of the

sunlight—which is the most universal effective and economical of all germicides

In Yorubaland, on the West Coast of Africa, Mr Alvan Millson calculated that about 62 233 tons of subsoil are brought every year to the surface of each square mile and that every particle of earth, to the depth of two feet, is brought to the surface once in twenty seven years It need hardly be added that the district is fertile and healthy

Earthworms play their part in the disintegration of rocks, letting the solvent humus-acids of the soil down to the buried surface Their castings on the hill slopes are carried down by wind and rain and go to swell the alluvium of the distant valleys or the wasted treasures of the sea The well known parallel ledges along the slopes of grass clad hills are partly due to earthworm castings caught on sheep tracks, and thus we begin to connect the earthworms not only with our wheat supply but with our scenery Well may we say, with Darwin "It may be doubted whether there are many other animals which have played so important a part in the history of the world as have these lowly organised creatures Those who wish to understand Darwinism should always begin with Darwin's last book—*The Formation of Vegetable Mould through the Action of Worms* (1881) It illustrates the web of life the idea of which is essential to an understanding of the struggle for existence and natural selection But it also illustrates what Darwin had learned from Lyell—that great results may be brought about by accumulation of infinitesimal items As Professor A Milnes Marshall said The lesson to be derived from Darwin's life and work cannot be better expressed than as the *cumulative importance of infinitely little things*

Termites, or white ants —Henry Drummond in his *Tropical Africa*, tried to make out a case for the agricultural importance of termites, or white ants It is well known that these old fashioned insects have a pruning action in the forest, destroying dead wood with great rapidity Houses and furniture, fences and boxes as well as forest trees fall under their jaws In some places "if a man lay down to sleep with a wooden leg it would be a heap of sawdust in the morning But what of the termites agricultural importance? The point is that they keep the soil circulating by constructing earthen tunnels up the sides of trees and posts and by making huge obelisk like ant hills, or termitaries "The earth tubes crumble to dust which is scattered by the wind the rains lash the forests and soils with fury and wash off the loosened grains to swell the alluvium of a distant

valley' It must be noted however that Drummond did not prove his case with sufficient precision and there is, as Escherich points out in his beautiful study of termites this difficulty that while the castings of earthworms are soft and loose the earth tubes and constructions of termites are stony

Escherich does however admit that the termites have some agricultural importance and he points out that there are other services to be put to the credit side of their account. They prune off wood that has begun to go they destroy rotting things, including the bodies of small animals, they make for cleanliness and health In some low lying tracts as Silvestri has shown there are dry stretches termite islands . which have been gradually built up from the broken-down remains of termitaries Nor should it be forgotten that the white ants are often used as food On the other hand Eschérich does not hesitate to rank them as among the great hindrances to the spread of civilisation They insidiously devour everything wooden from the telegraph post to the wooden butt of the gun hanging against the wall from books in the library to corks in the cellar There does not seem sufficiently precise information in regard to the living plants that *they attack and no safe general statement can be made except* that their appetite is large and catholic

With a centre in earthworms what a variety of interests must be included within the radius of their life and work!—centipedes birds moles seedlings man The same is true of termites and two further illustrations may be given Observers have reported about thirty different species of termites with the habit of feeding on fungi grown within the termitary on specially constructed mazy beds The habit is interesting in many ways for instance because the fungi afford a supply of nitrogenous material which is scarce in the ordinary diet of wood and also because a similar habit occurs in the quite unrelated true ants Finally the web is illustrated by the numerous boarders mostly beetles that are found in the termitaries—not hostile intruders or parasites but guests which are fed and cared for apparently for the sake of a palatable exudation with a pleasant narcotising effect on the termites With a centre in termites what a variety of interests must we not include within the radius of their life and work!—fungi and trees beetles and birds lizards and anteaters and man more than any

The hand of life upon the earth —The hand of life has been working upon the earth for untold ages . Take plants for instance The seaweeds lessen the force of the waves the lichens eat into the

rocks, the mosses form huge sponges on the moors which keep the streams flowing in days of drought Many little plants are forever smoothing away the wrinkles on the earth s—their mother's—face, and they adorn her with jewels Others that have formed coal have enriched her with ages of entrapped sunlight The grass—which began to appear in Tertiary ages—protects the earth like a garment, the forests affect rainfall and temper climate, besides sheltering multitudes of living things to many of whom every blow of the axe is a death knell No plant, from bacterium to oak tree, lives or dies to itself, or is without its influence upon the earth So among animals there are destructive borers and burrowers and conservative agents, such as the coral polyps and the chalk forming Foraminifera

Practical importance of a realisation of the web of life —What has Darwinism to do with human life? The answer at this stage in our inquiry is clear we must respect the web of life if we wish to master Nature She must be humoured, not bullied Emerson included in his vision of a perfected earth the absence of spiders, but the absence of spiders—which snare so many injurious insects—would mean the absence of much else man probably included In a northern county in Scotland the proprietors were justly annoyed at the injuries inflicted on young trees by squirrels and they formed a squirrel club setting a price on the beautiful rodent s head Perhaps a wiser course would have been to begin by inquiring what disturbance of the balance of nature had allowed the squirrels to multiply so disastrously But after a period of squirrel slaughter and some jubilation thereat a cloud began to rise in the sky The wood pigeons were multiplying worse than ever, and the farmers at least said with no uncertain voice that they preferred the squirrels An imperfect recognition of the web of life had left out of account the notable fact that squirrels destroy large numbers of young wood pigeons

One of the hopeful symptoms of the last few years is the reawakening of an interest in woods and forests Everyone knows how terribly these have been wasted, and how the disastrous results have affected rainfall and irrigation, climate and crops and even the character of the people Here what was once a pleasant stream is now like a gravelly road and there the fertile plains are flooded, here the wind is sweeping away the soil, and there both beauty and health have departed The birds which the woods once sheltered are driven elsewhere and the insect pests are rife among the crops For "the cheapest and most effective insecticides are birds [1]

The recognition of consequences—often far reaching—grows with us as we work with the idea of the web of life as we see in proper perspective the criminality of those who are ruthless President Roosevelt has declared his abomination of the land skinner' — 'the individual whose idea of developing the country is to cut every stick of timber off it, and then leave a barren desert for the home maker who comes in after him That man is a curse and not a blessing to the country The prop of the country must be the man who intends so to run his business that it will be profitable to his children after him Every right thinking man, and especially those who have grasped the idea of the web of life will say with Roosevelt "I am against the land skinner every time

It may be said that man must exterminate a good deal if he is to go on peaceably with his business and it will be admitted that there has never been a strong enthusiasm humanitarian or otherwise against the elimination of rattlesnakes and such like The naturalist's answer is that every crusade should be carefully considered on its own merits, and that every careless and hasty destruction of life is to be condemned Even in regard to snakes killing may be carried too far Some creatures are, as it were on the fringes of the web while others occupy a position where many threads meet It is scientifically and aesthetically deplorable that birds like the great auk and mammals like the quagga should have been exterminated but it is practically much more deplorable that we have lost so many hawks and weasels and other members of that pertinacious army whose guerilla warfare keeps hundreds of more humdrum creatures up to the scratch and keeps vermin from becoming a plague Moreover, it is extremely difficult to tell what may be the consequences of exterminating any creature—remote as it may seem from the beaten track of human affairs One of the obvious lessons of Darwinism is that we should be slow to call any change unimportant Everything counts or may count A so-called unimportant animal is destroyed and no immediate ill effects are seen But who can tell?

Very pertinent for instance is the question What about the parasites that used to complete their life history in romantic routine in this extinguished animal? Have we extinguished the parasite also? Or is it waiting with a whip of scorpions to chastise mankind for their ignorance of Darwinism?

The practical importance of recognising the web of life has been proved by the heavy penalties which man has often had to pay for

disturbing the balance of nature, careless of results and ruthless of beauty, for not admitting that if we would master Nature we must first understand her. How much has Australia had to pay for the introduction of rabbits in 1860 or America for sparrows? Sometimes the introduction has been unconscious, and man has only to blame himself for letting the intruder take hold as in the case of the Phylloxera in France, or of the Colorado Beetle in Ireland. "Ignorance of nature," Mr A. H. S. Lucas says, "is costly. By disturbing the balance of nature man has introduced foes into his own household." Speaking of Australia he says: "How much is needed for the eradication of Bathurst Burr, Prickly Pear, Water hyacinth, Bramble and Sweetbriar, Codlin Moth, Waxy Scale, Pear Slug, and Red Spider, owing to carelessness or lack of knowledge in early days?"

An obvious moral is that we should be careful in our introductions of new organisms—man included—into new surroundings. The primary consequences may be predictable, but the secondary and the tertiary consequences—who is sufficient for these things? We have records of the unconscious introduction of rats into Jamaica, where they became a pest. To destroy them mongooses were imported, and the rats were soon checked. But the mongooses, having finished the rats, began to eat up the poultry and young birds of various kinds. As this went on the injurious insects and ticks, that the birds used to eat, began to gain the ascendant. A recent report—which requires confirmation—says that the increase of ticks is making life a burden to the mongooses. Thus a balance will be again arrived at. There is no doubt of that, but how much is often unnecessarily lost by the way!

CHAPTER XXX

NATURAL SELECTION

In the Appendix will be found a chapter of excerpts from Darwin's *Origin of Species*. In this chapter he offers four objections to his theory and attempts to answer them. These four objections are not by any means all that Darwin foresaw, for he presented in another chapter a discussion of "Miscellaneous Objections to the Theory of Natural Selection." Before entering upon a general criticism of Darwinism it would be advantageous to have before us a brief and pointed summary of Darwin's theory—natural selection—now known technically as "Darwinism." The writer knows of no better short statement of the true content of Darwinism than the following summary by Professor Vernon L. Kellogg.

SUMMARY OF DARWIN'S NATURAL SELECTION THEORY

"Darwinism may be defined as a certain rational causo-mechanical (hence non-teleologic) explanation of the origin of new species. The Darwinian explanation rests on certain observed facts, and certain inductions from these facts. The observed facts are (1) the increase by multiplication in geometrical ratio of the individuals in every species, whatever the kind of reproduction which may be peculiar to each species, whether this be simple division, sporulation, budding, parthenogenesis, conjugation and subsequent division, or amphimixis (sexual reproduction); (2) the always apparent slight (to greater) variation in form and function existing among all individuals, even though of the same generation or brood; and (3) the transmission, with these inevitable slight variations, by the parent to its offspring of a form and physiology essentially like the parental. The inferred (also partly observed) facts are: (1) a lack of room and food for all these new individuals produced by geometrical multiplication, and consequently a competition (active or passive) among those individuals having any ecologic relations to one another, as for example among

From V. L. Kellogg's *Darwinism To-Day* (copyright 1907). Used by permission of the publishers, Henry Holt & Company.

those occupying the same locality, or needing the same food, or needing each other as food, (2) the probable success in this competition of those individuals whose slight differences (variations) are of such a nature as to give them an advantage over their confrères which results in saving their life at least until they have produced offspring and (3) the fact that these "saved" individuals will, by virtue of the already referred to action of heredity, hand down to the offspring their advantageous condition of structure and physiology (at least, as the "mode" or most abundantly represented condition among the offspring)

'The competition among individuals and kinds (species) of organisms may fairly be called a struggle This is obvious when it is active as in actual personal battling for a piece of food or in attempts to capture prey or to escape capture, and less obvious when it is passive as in the endurance of stress of weather hunger, thirst, and untoward conditions of any kind The struggle is or may be, for each individual threefold in nature (1) an active struggle or competition with other individuals of its own kind for space in the habitat, sufficient share of the food, and opportunity to produce offspring in the way peculiar and common to its species, (2) an active or passive struggle or competition with the individuals of other species which may need the same space and food as itself or may need it or its eggs or young for food and (3) an active (or more usually passive) struggle with the physico-chemical external conditions of the world it lives in as varying temperature and humidity storms and floods, and natural catastrophes of all sorts For any individual or group of individuals any of these forms of struggle may be temporarily ameliorated as is (1) the intra specific struggle among the thousands of honey bee individual living together altruistically, in one hive or (2) the inter specific struggle when two species live together symbiotically as the hermit crab *Eupagurus* and the sea anemone *Podocoryne* or (3) the struggle against untoward natural conditions as in special times or places of highly favourable climate, etc. Or for any individual or group of individuals all forms of the struggle may be coincidently active and severe The resultant of these existing conditions is, according to Darwin and his followers, an inevitable natural selection of individuals and of species Thousands must die where one or ten may live to maturity (i e, to the time of producing young) Which ten of the thousand shall live depends on the slight but sufficient advantage possessed by ten individuals in the complex struggle for

existence due to the fortuitous possession of fortunate congenital differences (variations) The nine hundred and ninety with unfortunate congenital variations are extinguished in the struggle and with them the opportunity for the perpetuation (by transmission to the offspring) of their particular variations There are thus left ten to reproduce their advantageous variations The offspring of the ten of course will vary in their turn but will vary around the new and already proved advantageous parental condition among the thousand say offspring of the original saved ten the same limitations of space and food will again work to the killing off before maturity of nine hundred and ninety leaving the ten best equipped to reproduce This repeated and intensive selection leads to a slow but steady and certain modification through the successive generations of the form and functions of the species a modification always toward adaptation toward fitness toward a moulding of the body and its behaviour to safe conformity with external conditions. The exquisite adaptation of the parts and functions of the animal and plant as we see it every day to our infinite admiration and wonder has all come to exist through the purely mechanical inevitable weeding out and electing by Nature (by the environmental determining of what may and what may not live) through uncounted generations in unreckonable time This is Darwin s causo-mechanical theory to explain the transformation of species and the infinite variety of adaptive modification A rigorous automatic Natural Selection is the essential idea in Darwinism at least in Darwinism as it is held by the present day followers of Darwin '

OBJECTIONS TO SELECTION

1 Darwin in a letter to his friend Hooker (January 11 1844) expresses his contempt of Lamarck s ideas in the following words Heaven defend me from Lamarck s nonsense of a tendency to progression 'adaptations from the slow willing of animals ' etc. Lamarck s work appeared to me to be extremely poor I got not a fact or idea from it '

In spite of these views Darwin s *Origin of Species* is interlarded with Lamarckian explanations Whenever the author feels the shortcomings of the selection factor he lapses into an explanation involving the idea that the effects of use and disuse of organs are inherited Followers of Darwin especially Weismann felt this to be the chief defect in the fabric of Darwinism and bent their efforts chiefly toward purging Darwinism of all taint of Lamarckism.

2 Darwin insisted upon the idea that minute fluctuating variations, which we now know are to a large extent non heritable were the principal if not the sole, materials for natural selection to work upon He knew of a considerable number of "sports" or "saltatory variations (now called mutations), but considered these too infrequent to furnish the necessary basis for selection We now know that mutations may be as small as fluctuating variations or as large as 'sports and that they are of much more frequent occurrence than Darwin supposed

3 Darwin considered all variations as heritable He did not distinguish between *somatic* variations and *germinal* variations. In fact, as we learn from a study of his pangenesis theory, he considered all variations as in the first instance somatic and subsequently transferred by means of gemmules to the germ cells Every somatic variation whether induced by use, disuse in response to environmental stimulus, or through mere spontaneous variability, was supposed to be able to give off gemmules into the blood stream that would carry to the germ cells the physical basis of the varying character The pangenesis mechanism is now known to have no basis in fact

4 The natural selection theory is based upon a mistaken conception of the methods of artificial selection Darwin believed without having any proof for this belief, that the way in which domestic varieties had been so profoundly modified at the hands of man was by the conscious or unconscious selection of slight fluctuating variations in favorable or desired directions and that this resulted in the cumulative improvement or enhancement of the desired characters over a long series of generations Darwin supposes that the radically changed conditions of domestication hasten and stimulate variability, thus offering a better opportunity for selection Transferring this idea to nature, he thinks that changed natural conditions stimulate variability, just as does domestication, and that this is seized upon by natural selection to make for adaptation to the new environment and the resultant origin of new species

Our modern experimental studies have shown that somatic modifications due to environmental changes are not hereditary, and that all of the recent domestic varieties whose origin has been observed have been the result of suddenly appearing germinal variations or mutations that arrive fully formed and cannot be improved by selection except that they usually need to be selected out or isolated in

order to prevent swamping out through intercrossing with the parent type

5 Objection has frequently been made to Darwin s idea of the purely fortuitous or chance character of variations According to this view variations occur in all structures and in all directions at haphazard so that there would be the widest possible opportunity for a given adaptive variation to occur just when the circumstances would demand It now appears that variations do not occur in all directions in random fashion but that they tend to follow certain definite paths of change in other words, variations are to a considerable extent at least orthogenetic If variations really tend to follow certain definite lines owing to purely internal causes natural selection would be unnecessary at least until orthogenesis went too far for the good of the species or far enough to be of real importance in the struggle for existence

6 The difficulty of explaining how natural selection could make use of the initial stages of adaptive structures is obvious It is inconceivable that the first almost imperceptible variation in a favorable direction could be of selective value, so as to effect the survival of the individual or the relative number of its offspring What would be the advantage of the first few hairs of a mammal or the first steps toward feathers in a bird when these creatures were beginning to diverge from their reptilian ancestors? This objection is of course based on the fluctuating variation idea If the mutation idea were substituted the difficulty would to a great extent clear up for a mutation might be of sufficient importance in one generation to have selective value from the very first

7 Natural selection is said to be incapable of explaining the origin of coadaptive and highly complex adaptations whose effectiveness depends upon the perfection of their adjustments to one another For example we may refer to some of the perfected adaptations described in chapter xiv In the case of the electric organs of certain fish the Darwinian assumption would be that the first step in the direction of an electric organ would be a very small one and that it was built up little by little by means of natural selection But say the critics the electric organ would be of no value until it became powerful enough to impart an effective shock to the intruder and this would not be possible if the character began in a small way The whole phenomenon of protective resemblance is open to the same type of criticism As a specific example of this we may cite the case of the dried leaf

butterfly *Kallima* previously described (pp 226–228) In its present condition this animal has a strikingly detailed resemblance to a dried leaf which is therefore doubtless of some value But of what value would be the first tiny change in the direction of resemblance? Until its resemblance became close enough actually to deceive the enemies of butterflies, the critics claim there would be no chance for selection to act.

8 It is frequently objected that a vast number of characters of organs are useless or non adaptive and, as such could not have arisen through the instrumentality of natural selection If these useless characters which are sometimes quite large and prominent, are independent of natural selection, why do we need natural selection to explain adaptive characters? It is also claimed that a vast number of specific peculiarities are useless and therefore could not have helped in the differentiation of species It should be said in defense that Darwin realized this difficulty quite as clearly as do his critics and was greatly puzzled by it His idea of correlated variability, however helps to answer it for it may well be that many of these apparently useless characters are correlated or linked in inheritance, with characters of supreme selective value such as general hardiness or great fecundity Darwin also points out that we are not in a position at present to pronounce judgment on the value of many structures or functions that have been adjudged non adaptive

9 Certain characters in organisms past and present have been interpreted as overspecializations, organs that have evolved beyond the range of usefulness or that are more elaborate than is demanded for survival under the conditions of life The case of the extinct Irish elk is often cited as an example of overspecialization This group of animals went to extremes in the development of size and elaboration of horns far beyond the range of usefulness so that it is said to have brought about the extinction of the race Natural selection, which is supposed to have brought the horns up to the point of adaptive perfection, should have kept them within the bounds of usefulness

Again the enormously overgrown and overspecialized dinosaurs of long ago are thought of as having followed their lines of evolution far beyond the point of greatest effectiveness and adaptability

10 The rudimentation of structures which is such a common phenomenon in nature is said to meet with no adequate explanation on a selection basis The case of the whale s vestigial hind limbs is a case in point Darwin s explanation would be that under aquatic conditions the first whale ancestors would be handicapped by hind

legs and that any decrease in their size which would be enhanced by disuse would be of advantage. This might seem reasonable during the main period of limb reduction, but, after the limb is reduced to a subcutaneous rudiment, there could be little advantage in carrying the rudimentation still farther. Some whales have the hind limbs much more profoundly reduced than others although they are all thoroughly out of the way and involve no hindrance in swimming. Any number of similar cases of the same kind might be cited. Darwin had no explanation to offer except a resort to Lamarckism but Weismann the ablest neo-Darwinian offered the theory of panmixia to cover this objection a theory which is mentioned in chapter 1 and will be discussed later.

11 It is objected that unless favorable variations occur in a large number of individuals at the same time the character would be swamped out by intercrossing with individuals not possessing the favorable variation. The probability that such a swamping-out would occur was shown mathematically by various critics. By way of answer to this objection there arose a number of isolation theories, according to which favorably varying individuals would be protected from back-crossing with the non varying individuals. We might also point out that the Mendelian laws of dominance and segregation would serve to prevent loss of any new favorable character.

12 It is objected that natural selection might explain the survival but not the arrival of the fittest. But Darwin met this perfectly when he said "Some have even imagined that natural selection induces variability whereas it implies only the preservation of such variations as arise and are beneficial to the being under its conditions of life."

13 Criticism has been directed against natural selection because of the fact that some of the supporters of Darwinism notably Weismann, have made the claim that natural selection is the sole cause of evolution. This idea of the *Allmacht* or all-sufficiency of natural selection was not Darwin's as is clear from the following statement: "I am convinced that natural selection has been the most important, but not the exclusive means of modification."

14 It is objected that many if not most of the fluctuating variations with which Darwinism deals are purely quantitative or plus-and minus variations, whereas the differences between species are qualitative. This is a serious objection and difficult to meet yet a fair defense has been formulated by leading neo-Darwinians.

15 There is a growing skepticism on the part of biologists as to the extreme fierceness of the struggle for existence and of the consequent rigor of selection It may be answered that no very obvious fierceness is implied in the theory So long as overproduction and a shortage of space and food exists the struggle for existence is inevitable

16 Special objections are offered to the subsidiary theory of sexual selection It is said that the type of sexual selection involving active rivalry and battling for mates needs no special theory, inasmuch as this is a mere phase of the struggle for the maintenance of the full life, including the chance to leave offspring It is against the other side of sexual selection, which involves passivity on the part of the male and active choice on the part of the female of the more beautiful or otherwise attractive male that objection is raised It is claimed that such choice implies too high aesthetic powers in animals of relatively poor vision and mentality Experiments have been performed with moths in which the male and female coloration is strikingly different in order to determine whether females actually do exercise any choice of mates that is based on considerations of appearance The result proved conclusively that color patterns have no value in mating but that the female is passive and mates with the first male to present himself, while the male finds the female through his exquisitely effective sense of smell

We know now however that secondary sexual characters are intimately bound up in a physiological way with the functioning of the sex glands and are therefore doubtless to be interpreted as mere non adaptive correlative variations or else as examples of obliterative coloration.

DEFENSE OF SELECTION

In presenting these sixteen objections, we have in most cases indicated the lines upon which the objections have been met, if they have been met. Not all of these objections are considered serious at the present time, for some are based upon lack of a full knowledge of what Darwin actually wrote others are largely academic in character and fail to stand up under actual test still others have been more or less adequately met by subsidiary or supporting theories which have been advanced by various neo-Darwinians

Most of the special objections raised in this chapter have received the attention of various able Darwinians and the student of evolution would doubtless be interested in the expert and fair minded defense

of Darwinism at the hands of Professor V L Kellogg as it appears in his book *Darwinism To Day*

A much briefer and considerably more general defense is that of J L Tayler, which is as follows

GENERAL DEFENSE OF SELECTION

J L TAYLER

To realise how far the theory of selection is capable of explaining the facts of organic evolution it is necessary to bear in mind the postulates in which the theory is founded

1 It is obvious that natural selection can only act by preserving or eliminating the complete organism Selection must therefore be organismal This Darwin and other selectionists have clearly recognised

2 As the whole organism must survive if the favourable variation or variations are to be preserved it follows that certain minor unfavourable variations may also be preserved if they happen to exist in an individual which survives on account of its major favourable variations And since no individual is completely adapted to its environment it follows that there must be always a variable amount of residual unfavourable variability in every organism

3 This residual unfavourable variability may be of considerable utility under changed conditions

4 Complementary specialisation of parts as Spencer has shown is favourable to successful competition and as it is the whole organism that is selected or eliminated it follows that any weakness of one specialised part since it would disturb the balance of all, would be detrimental The more complex the organism the more specialised the structures the more dependent one part will be on the others for its existence hence a complementary specialising tendency will be favoured by selection and therefore all struggles of one part of an organism with another will be reduced to a minimum

It is clear that there must be some underlying criterion which determines whether any given organism shall be selected or not and that criterion must be the net result of its adaptability to its environment One organism may conceivably survive by its possession of a large number of small favourable variations while another may survive in virtue of a single valuable one but in each case it would be

From J L Tayler The Scope of Natural Selection " Natural Science 1899

the whole value of that organism which determined its survival This fact is continually disregarded by opponents of the neo Darwinian position yet this selection of the organism as a whole is the fundamental postulate from which the theory of selection starts Thus it is not uncommom to read criticisms bearing on the early development of some organ, in which the inadequacy of selection is supposed to be proved by the writer demonstrating or believing he has demonstrated the fact that the particular variation in question must have been too small to be by itself of selection value In many cases the particular variation would, no doubt, if taken alone be as the objector asserts too unimportant to be selected but as it is the whole organism that is selected it is not logical to make an artificial separation and study the development of one organ or structure irrespective of the other organs with which it is in nature associated *Every organ in its evolution must be considered in relation to the whole of the particular organism in which that particular stage of development of that organ is found*

Starting therefore with this fact that the net value of adaptability of the whole organism to its environment must be the basis which determines selection or elimination, it will follow that certain lines of development will result from the application of this criterion In a series of organisms placed under new conditions, elimination will proceed along lines essential to bring about a proper adjustment to the new conditions If the offspring of these adjusted organisms merely repeated in their generation the characters of the exterminated as well as of the surviving organisms that temporary adjustment would be permanent as long as the conditions were unchanged But since the offspring are produced only by the surviving organisms selection is continually raised to higher and higher planes of adaptation, and therefore as long as conditions remain constant, the tendency of selection must be, as Darwin clearly saw, cumulative He did not, however apparently see that from this cumulative tendency definite variability must arise out of indefinite

Selection in direct relation to climatic conditions is therefore of very minor importance, while selection among the members of a species and all forms of inter-organismal selection is of infinitely more importance since it is this interaction, produced by the offspring in different degrees inheriting the advantages of both parents (both of whom have survived on account of certain advantages) that leads to the cumulative development and never ending struggle for survival

Darwin came very near to this conception of definite variability when he pointed out that ' if a country were changing the altered conditions would tend to cause variation not but what I believe most beings vary at all times enough for selection to act on Extermination would expose the remainder to the mutual action of a different set of inhabitants which I believe to be more important to the life of each being than mere climate and as the same spot will support more life if occupied by very diverse forms ' it is evident that selection will favour very great diversity of structure

Bearing in mind this cumulative action of selection it will follow that under constant or relatively constant conditions the struggle for successful living will become more and more selective in character even if the actual number of inhabitants remain more or less the same as when the struggle first commenced The selection of variations will thus tend to pass through certain more or less ill-defined but nevertheless, real stages In proportion as the struggle becomes intense either from the number or from the increasing adaptability of the organisms or both certain major essential adaptations which were necessary for the climatic and other more or less comparatively simple conditions will be supplemented by minor auxiliary variations which in the earlier stages would not have appeared And still later as more and more rigorous conditions of life were imposed the advantage would tend to rest with those organisms which possessed highly co-ordinated adaptations, since this would entail more rapid responsiveness to environment.

As evolution advances from the unspecialised to the specialised and higher and higher forms of life come into being with increasing complexity and specialisation of parts entailing an increasingly delicate adjustment of those parts to each other s needs the relation of each part to the whole organism becomes of more and more importance and it follows that selection must become more and more generalised in its action No single variation could be of service to any of the higher forms of life unless it was in more or less complete harmony with the whole tendency of the individual The adjustment of parts and their mutual interdependence make it essential for adaptation that the relation of parts be preserved consequently correlated minute favourable variations will tend to be more and more selected as evolution passes from the unspecialised to the specialised forms of life This response of the whole organism should be still more delicate in those forms of life that are continually subjecting themselves to

changed conditions hence this delicacy of adjustment is far more necessary in the higher forms of animal life than in more stationary plant organisms and in the developing nervous systems of animals we have just the central adjusting system that is required for these conditions *With evolution of type there will thus be an increasingly definite tendency given to organic especially the animal, forms of life if the acting principle of evolution has been selectional Selection is, therefore able to account for the steadily progressive tendency of life as a whole without calling to its aid any unknown and doubtful perfecting principle*

To summarise Natural selection acting on the whole organism tends to produce more and more definite tendencies in all surviving forms of life which tendencies are progressive and continuous in character Variable conditions by partially altering the line of selection, induce a temporary indefiniteness And lastly the process of selection being itself able to be the indirect, though not the direct cause of those favourable variations which it subsequently selects from is able to dispense with any subsidiary factors provided it has a certain number of elementary properties of life which afford sufficient material to work with

EXPERIMENTAL SUPPORT OF THE EFFECTIVENESS OF NATURAL SELECTION

Weldon's experiments with the shore-crabs of Plymouth Sound — These experiments seem to show that under changed environmental conditions natural selection acts upon minute fluctuating variations of linear or quantitative type so as to produce an alteration in the species exactly as Darwinism would hold A large breakwater was so placed near the mouth of Plymouth Sound that the rate of flow of the river water was greatly slowed down in certain regions This allowed an increased settling of the fine china clay sediment that is carried by the river and the changed condition caused the death of numerous crabs of the species *Carcinus maenas* The question arose as to whether the survivors and those that had perished showed any consistent differences on the basis of which selection could be operating Careful measurements of hundreds of individuals showed that the mean breadth of frontum is slightly less in the survivors than in the perished Measurements were repeated in two subsequent years and it was found that there was a progressive narrowing of the frontum As an experimental check upon these conclusions Weldon

placed a number of crabs in a large aquarium in which china-clay w kept partly in suspension and found that about half of them die Again the survivors were compared statistically with the perished an the same relation was found to hold, that the survivors had a me frontal breadth distinctly narrower than that of the perished Wi don concludes that his experiments have demonstrated two fac about these crabs: the first that their mean frontal breadth is dimi ishing year by year at a measurable rate which is more rapid in mal than in females the second is that this diminution in frontal bread occurs in the presence of a material namely fine mud which increasing in amount and which can be shown experimentally destroy broad fronted crabs at a greater rate than crabs with narrow frontal margins and I see no escape from the conclusi that we have here a case of Natural Selection acting with gre rapidity because of the rapidity with which the conditions of l are changing

Cesnola s experiments with Mantis —To test the selective val of color markings Cesnola fixed specimens of the brown and gre *Mantis religiosa* on plants some of which were against harmoniou others against disharmonious backgrounds The result was that mo of those which were inconspicuous because of a harmonious bac ground escaped while most of the others were eaten up by birds

Poulton s and Sanders' experiments with butterfly pupae Numerous pupae of various colors were placed under conditions favo ing protective coloration and others under opposite conditions; T conclusion was that protective coloration is a real survival factor an one that operates so as to give the protectively colored individu a decided advantage in the struggle for existence

Davenport s experiments with chickens —A number of chicken some black some white and some barred or checkered in color we allowed to wander free in the fields Hawks killed most of the whit and many of the blacks but spared to a large extent the less co spicuous checkered and barred types which are harder to dete against a mixed background

All of these experiments merely tend to show that discrimina survival actually occurs but only the experiment of Weldon has bearing on the possibility that mere quantitative changes of sm dimensions might under certain conditions be of selective value V badly need more experimental evidence of this sort and until th is forthcoming we shall have to admit that there is very litt

experimental evidence in favor of the type of natural selection that Darwin stood for

THE PRESENT STATUS OF NATURAL SELECTION

It has come to be rather generally believed that the natural selection that Darwin himself believed in stands almost unscathed as one very important causal factor In fact it is the only explanation ever offered for adaptation that even approaches adequacy As an explanation of the origin of new types or new species it falls far short of adequacy and I think Darwin evidently realized this although he was unfortunate enough to entitle his book *Origin of Species* As an explanation of the origin and perfection of adaptation natural selection has only one rival, the far less satisfactory Lamarckian theory of the inheritance of acquired characters There is a strong tendency among geneticists to conclude that the modern germ plasm hypothesis with the aid of mutations and the mechanism of Mendelian inheritance, furnishes all the necessary explanation of the causes of evolution There is however, marked dissent to this extreme position In his critique of De Vries s rather extreme position that the mutation theory needs no aid from natural selection, Weismann shows in most able fashion the inadequacy of mutations to account for adaptation and in contrast how well natural selection accounts for them

In a very recent paper Professor C C Nutting attempts to show that natural selection is still an important factor in evolution and quite in harmony with both the mutation theory and Mendelism We perhaps can close the present chapter no more fittingly than by quoting Professor Nutting s paper

THE RELATION OF MENDELISM AND THE MUTATION THEORY TO NATURAL SELECTION[1]

C C NUTTING

Two marked tendencies are evident in the history of any important theory after its publication

First The followers of the discoverer carry the theory too far and attempt too universal an application This is manifestly true of Wallace and Weismann who out Darwined Darwin in their claims for natural selection, of the followers of Mendel such as Morgan and

[1] From an address given before the Genetics branch of the American Association for the Advancement of Science December 1920 *Science* N S Vol. LIII

Pearl, and of many mutationists who make much greater claims for that theory than does De Vries himself

Second Each generation of biologists is so occupied with its own work and contemporary theories that it makes no real effort to understand preceding theories

This second tendency seems to me most marked in the attitude of present workers along genetic lines towards natural selection. They reveal an apparent lack of understanding of what Darwin really meant and of what he claimed and when criticising that theory they are often engaged in the classic but unprofitable exercise of fighting windmills

In view of these facts I hope you will pardon me if I present in as few words as possible just what I believe to be the main factors which Darwin presented as resulting in their actions and reactions in natural selection These factors are three in number

First *Heredity* by which the progeny tend to resemble their parents more than they do other individuals of the same species

Second *Individual variation* by which the progeny tend to depart from the parental type and sometimes from the specific type

Third *Geometrical ratio* of increase by which each species tends to produce more individuals than can survive

Each of these factors is practically axiomatic so little is it open to argument

No one doubts the fact of heredity whether pangenesis Weismannism or Mendelism be the correct expression of the mechanism involved. These do not affect the fact of heredity nor invalidate it as a factor in natural selection

No one doubts the fact of variation whether it is the individual variation of Darwin the fluctuating variety or the mutation' of De Vries. All that is necessary for Darwin s purpose is that there be heritable variations That there are such things all parties agree and it matters little what you call them They are adequate to act as a factor in the Darwinian scheme

No one doubts the fact of geometrical ratio of increase It is a proposition easily capable of mathematical demonstration and that is sufficient for Darwin s purpose

These three factors then are not debatable as facts whatever their mechanism or causes

A moment s reflection will show that geometrical ratio of increase is a quantitative factor giving an abundance of individuals from

which to select that individual variation is a qualitative factor giving the differences which make a selection possible and that heredity is a conservative factor, holding fast those characters which better fit the organism to its environment

Now it seems to me that there is no possible outcome of the necessary action and interaction of these three factors that would not be a selection of some sort Darwin thought it comparable in a large way to the selection by which the stock breeder improves his herd, and therefore called it ' natural selection ' carefully guarding the phrase from misinterpretation from the teleological angle as well as from a too close parallelism between artificial and natural selection And I believe no one has suggested a more acceptable term for the process of selection resulting from the interplay of natural laws

Three outstanding theories have been advanced since the publication of the *Origin* each involving an advance in our knowledge of the mechanism of heredity on the one hand and the origin of variations on the other

Weismann's theory of the continuity and stability of the germ plasm was of immense importance in its discussion of the mechanism of heredity, and his amphimixis gave a plausible explanation of the origin of variations His results were almost universally regarded as confirming and greatly extending the scope of natural selection

Mendel s theory regarding the purity of the gametes, their segregation in the sex cells and the whole complex Mendelian mechanism so admirably described by Morgan all of these, fascinating and important as they are deal with the mechanism rather than the fact of heredity In my opinion their acceptance or rejection does not affect the status of natural selection as a theory of organic evolution

But it is the theory of mutation that has furnished most of the ammunition for the opponents of natural selection, and this in spite of the fact that De Vries, the originator of the mutation theory, expresses himself with great clarity as follows

' My work claims to be in full accord with the principles laid down by Darwin and to give a thorough and sharp analysis to some of the ideas of variability inheritance, selection and mutation which were necessarily vague in his time "

In 1904 when these words were published there did seem to be a sharp distinction between the ideas of Darwin and those of De Vries The former believed that natural selection acted upon many small variations and accumulated them until the differences were sufficient

to constitute new species while De Vries claimed that new species were formed by the sudden appearance by mutations of forms specifically distinct from the parents; That mutants were new species!

It seems evident that Darwin did not regard saltatory evolution as the common method while De Vries did

Darwin believed that individual usually small variations furnished the material on which selection acts; while De Vries thought that mutants usually large variations furnished the material Both however believed thoroughly that natural selection was a *vera causa* of evolution

But things have changed greatly since 1904 The work of Morgan Castle Jennings and a host of others has shown that many mutations are so small from a phenotypic standpoint that they are quantitatively no greater than the individual variations of Darwin and that they are heritable in the Mendelian way

Castle produced a perfectly graded series of hooded rats which exhibits almost ideally the steps by which a new form might be produced by natural selection He says

If artificial selection can in the brief span of a man s lifetime mould a character steadily in a particular direction why may not natural selection in unlimited time also cause progressive evolution in directions useful to the organism?

Jennings says

Sufficiently thorough study shows that minute heritable variations—so minute as to represent practically continuous gradations—occur in many organisms some reproducing from a single parent others by biparental reproduction It is not established that heritable changes must be sudden large steps; while these may occur minute heritable changes are more frequent Evolution according to the typical Darwinian scheme through the occurrence of many small variations and their guidance by natural selection is perfectly consistent with what experimental and paleontological studies show us to me it appears more consistent with the data than does any other theory

Many believers in mutation have been needlessly befuddled by the diverse meanings of variations as used by Darwin and De Vries Darwin included in his individual variations both the 'fluctuating varieties and the mutations of De Vries Phenotypically they cannot even now be distinguished De Vries himself candidly admits that this was Darwin s attitude thus proving himself

more clear sighted than many of his followers All that Darwin needed for his purpose was proof of variations that are heritable, and these are found in mutations be they large or small

Just as Mendelism has to do with the mechanism and not the fact of heredity, so the mutation theory deals with the nature and not the fact of variations Neither, in my opinion, has any implication that is antagonistic to the theory of natural selection

The statement has been made that natural selection ' originates nothing because it does not explain the origin of variations I must confess scant patience with this point of view As well say that the sculptor does not make the statue because he does not manufacture the marble or his chisel or that the worker in mosaic originates nothing because he does not make the bits of stone which he assembles in his design!

The material corresponding to the bits of stone in the mosaic is furnished by heredity and variation and its quantity by geometrical ratio of increase Natural selection acts in selecting and putting together this material in the formation of new species Thus in a true sense it seems evident that something new has appeared—something that is but was not

Another favorite figure introduced I believe by De Vries is Natural selection acts only as a sieve determining which forms shall be retained and which shall be discarded This also seems to me to fall short of a complete statement of the truth If the material subjected to the sifting process be regarded as changing with each generation by the addition of variations or mutations if you prefer some of which are favorable to a nicer adjustment of the species to its environment the figure would be more nearly correct. To make it complete, however the mesh of the sieve must change from generation to generation so that a quantitative variation which would be preserved in one generation would be discarded in a later one But in this case natural selection would do more than a sieve could do It would combine a number of favorable variations in the production of something new a new species!

In conclusion it seems to me that we are justified in maintaining that Mendelism and the mutation theory while forming the basis of the most brilliant and important advances in biological knowledge of the last half century, have neither weakened nor supplanted the Darwinian conception of the ' Origin of species by means of Natural Selection.

CHAPTER XXXI

ARE ACQUIRED CHARACTERS (MODIFICATIONS) HEREDITARY?

INTRODUCTORY NOTE —In a previous chapter (chap xvi) under the heading Heredity in Pure Lines it was pointed out that germinal variations are hereditary and somatic variations (modifications) are not hereditary That germinal variations are hereditary and may be produced in a number of different ways was also made clear in the discussion of mutations but the statement that somatic modifications are never in the least hereditary is equivalent to a total denial of the doctrine of the inheritance of acquired characters the so-called Lamarckian theory which was briefly presented in chapter ii

This is not a closed question and the final answer has been given neither in the negative nor in the affirmative The problem is of utmost import for evolutionists and for all who are interested in race improvement. So important is it to view this question fairly that we shall quote extensively from several of the leading students of the problem

MISUNDERSTANDINGS AS TO THE QUESTION AT ISSUE

J ARTHUR THOMSON

The precise question is this *Can a structural change in the body induced by some change in use or disuse or by a change in surrounding influence affect the germ-cells in such a specific or representative way that the offspring will through its inheritance exhibit, even in a slight degree the modification which the parent acquired?*

Before we pass to discuss the evidence pro and con it will be useful to notice some frequently recurring *misunderstandings* the persistence of which would make further argument futile

Misunderstanding I —*How can there be progressive evolution if acquired characters are not transmitted?*—Those who have not thought clearly on the subject often shake their heads sagely and remark that they do not see how evolution could have been possible at all unless what is acquired by one generation is handed on to the next To this we have simply to answer (1) that our first business is to find out the facts of the case careless whether it makes our interpretation of the history of life more or less difficult and (2) that in the supply of germinal *variations* whose transmissibility is unquestioned there is ample raw material for evolution We know a little about the abundant

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crop of variations at present supplied there is no reason to believe that it was less abundant in the past

Misunderstanding II —*Interpretations are not facts* —There are many adaptive characters in plants and animals which may be superficially interpreted as due to the direct result of use and disuse or of environmental influence The Lamarckians have so interpreted them and the Lamarckian way of looking at adaptations has become habitual to many uncritical minds They see on modern flowers the footprints of insects which have visited them for untold ages, they speak of the dwindling of the whale s hind limbs through disuse of the hardening of the ancestral horses hoofs as they left the marshes and ran on harder ground they picture the giraffe by persistent effort lengthening out its neck a few millimetres every century as the acacia raised its leaves higher and higher off the ground and they say that animate nature is so full of evidences of the inheritance of acquired characters that no further argument is needed

But all this is a begging of the question It is easy to find structural features which *may be interpreted* as entailed acquired characters if acquired characters can be entailed Obviously however we must deal with what we can prove to be modifications or with what we can plausibly regard as modifications because we find their analogues in actual process of being effected to-day

It is easy to say that the blackness of the negro s skin was produced by the tropical sun, and that it is now part of his natural inheritance It is easy to say this but absolutely futile Let us first catch our modifications

The Golden Rod (*Solidago virgaurea*) growing on the Alps is precocious in its flowering when compared with representatives of the same species growing in the lowlands Hoffmann found that Alpine forms transplanted to Giessen remained precocious therefore the acquired precocity had become heritable But there is no evidence that the precocity was acquired it may have been the outcome of the selection of germinal variations

The African Wart hog (*Phacochoerus*) has the peculiar habit of kneeling down on its fore limbs as it routs with its huge tusks in the ground and pushes itself forward with its hind limbs It has strong horny callosities protecting the surfaces on which it kneels and these are seen even in the embryos. This seems to some naturalists to be a satisfactory proof of the inheritance of an acquired character It is to others simply an instance of an adaptive peculiarity of germinal origin wrought out by natural selection

Misunderstanding III —*Begging the question by starting with what is not proved to be a modification* —There is no relevancy in citing cases where an abnormal bodily peculiarity re appears generation after generation unless it be shown that the peculiarity is a modification and not an inborn variation whose transmissibility is admitted by all Short sightedness may recur in a family series generation after generation but there is no evidence to prove that the original short sightedness was a modification In all probability short sightedness is in its origin a germinal variation like so many other bodily idiosyncrasies

In regard to some diseases such as rheumatism it is often said dogmatically by those who know little about the matter that the original affection in the ancestor was brought about by some definite external influence—such as a cold drive or a damp bed but it seems practically certain that in all such cases we have to do with an inborn predisposition to the expression of which the cold drive or the damp bed were merely the liberating stimulus comparable to the pulling of the trigger in a loaded gun The liberating stimulus is of course of great importance both in the case of the gun s discharge and the organism s disease but it only goes a little way towards a satisfactory interpretation in either case Not that we can explain the origin of rheumatism or shortsightedness or any such thing—there is no explanation in calling them germinal variations that cropped up but we are almost certain that they never are modifications or acquired characters

Herbert Spencer twits those who are sceptical as to the transmission of acquired modifications with assigning the most flimsy reasons for rejecting a conclusion they are averse to but when Spencer cites the prevalence of short sightedness among the notoriously studious Germans the inheritance of a musical talent and the inheritance of a liability to consumption as evidence of the inheritance of modifications we are reminded of the pot calling the kettle black

Over and over again in the prolific literature of this discussion the syllogism is advanced either in regard to gout or something analogous—

Gout is a modification of the body an acquired character

Gout is transmissible

Modifications are sometimes transmissible

It may be formally a good argument but there is every reason to deny the major premise There is no proof that the gouty habit had an exogenous origin—that it was to begin with for instance the direct result of high living though it is generally admitted that

excesses in eating or drinking may give a stimulus to its expression ' The conclusion that I have arrived at,' says Prof D J Hamilton, "is that the gouty habit of body has arisen as a variation, and as such is hereditarily transmissible and that excess of diet and alcohol merely renders the habit of body apparent ' It may also be pointed out that gout and rheumatism and the like are rather *processes of metabolism* than structural modifications though the latter may ensue

After pointing out the irrelevancy of citing cases of the hereditary recurrence of polydactylism haemophilia, colour blindness in man or the absence of horns in cattle or of tails in cats as instances of the transmission of acquired characters Prof Ernst Ziegler says ' Only that can be regarded as acquired which is produced in the course of the individual life during and after the period of development exclusively under the influence of external conditions the term is in no wise applicable to peculiarities which as one says arise of themselves from a predisposition already present in the germ

Misunderstanding IV —*Mistaking the reappearance of a modification for transmission of a modification* —It is of little service to cite cases where a particular modification reappears generation after generation unless it be shown that the change recurs *as part of the inheritance*, and not simply because the external conditions which evoked it in the first generation still persisted to evoke it in those that followed Reappearance is not synonymous with inheritance

Misunderstanding V —*Mistaking re infection for transmission* — A particular form of the fourth misunderstanding has to do with facts so special that it may be conveniently treated of separately It has to do with microbic diseases It is admitted that a parent infected with tubercle bacillus or with the microbe of syphilis may have offspring also infected But such cases are irrelevant in the discussion Infection, whether before or after birth, has nothing to do with inheritance As Dr Ogilvie says ' Wherever the transmission of infectious disease from parent to offspring has been adduced to support the doctrine of the inheritance of acquired characters, it has been done in utter misconception of its meaning and scope

Medical men have sometimes condescended to make a subtle distinction between hereditary and ' congenital ' syphilis—the latter manifested at birth, the former some time afterwards! It seems strange that they have failed to recognise that there is no reason to use the word ' hereditary ' at all in this connection What occurs is an *infection*, and it is theoretically immaterial at what stage the infection occurs A microbe cannot be part of an inheritance

Misunderstanding VI —*Transmission in unicellulars is not to the point* —It is not to the point to cite cases where unicellular organisms such as bacteria or monads, have been profoundly and heritably modified by artificial culture, so that for instance the descendants of a virulent microbe have been made to lose their evil potency It is irrelevant because in regard to unicellular organisms we cannot draw the distinction between body and germinal matter, apart from which the concept of modifications is of no value In artificial culture the whole character of the unicellular organism—its particular metabolism —is altered it multiplies by dividing into two or more parts which naturally retain the altered constitution But this is worlds away from the supposed case of an alteration in the structure of the little toe so affecting the germ cells that the offspring inherit a corresponding deformation

Professor L Errera (1899) reported an experiment with a simple but multicellular mould (*Aspergillus niger*) which adapted itself to a medium more concentrated than the normal The second generation of the mould was more adapted than the first and the adaptation to the concentrated medium was not wholly lost after rearing in the normal medium again This looks like evidence of the inheritance of the acquired adaptive quality which was brought about as a direct modification But the case does not really help us since the distinction between *soma* and *germ plasm* is not more than incipient in the mould in question And even if the distinction were more marked it would only show that the germ plasm is capable of being affected *along with* the body by a deeply saturating influence which nobody has ever denied

Misunderstanding VII —*Changes in the germ-cells along with changes in the body are not relevant* —Another misunderstanding is due to a failure to appreciate the distinction between a change of the reproductive cells along with the body and a change in the reproductive cells conditioned by and representative of a particular change in bodily structure The supporters of the hypothesis that modifications may be transmitted point to the tragic cases where some poisoning of the parent s system by alcohol opium or some toxin is followed by some deterioration in the offspring There is no doubt as to the fact the question is as to the correct interpretation

1 In some cases it may be that the whole system of the parent is poisoned—reproductive cells as well as body the effect may be as direct on the germ-cells as on the nerve-cells These therefore are not cases on which to test the transmissibility of an acquired character—i.e

of a particular somatic modification If a local poisoning had a structural effect on some particular organ and if that structural effect was reproduced in any degree in the offspring the case would be relevant but when the whole organism is soaked in a poison the case is irrelevant If it could be said that the sunshine which brings about sun burning in the skin soaks through the organism even to its reproductive cells and specifically affects them in a manner analogous to the saturating poison, we should have a physiological basis for expecting the inheritance of sun burning But we cannot make this assumption We have no warrant for believing that the modification of a part re-echoes in a definite specific way through the organism until even the penetralia of the germ cells reverberate

2 A parent organism is poisoned and there are structural results of that poisoning The offspring are born poisoned and show similar structural peculiarities This may be due to the fact that the germ cells were poisoned along with the parental body, but it may also be due, in the case of a mother to a poisoning of the embryo before birth in a manner comparable to a pre natal infection

3 In some cases—*e g* of alcoholism in successive generations—there may be poisoning of the germ cells along with the body, there may be poisoning of the embryo before birth and of the infant after but it may also be that what is really inherited is a specific degeneracy of nature an innate deficiency of control perhaps which led the parent to alcoholism, and which may find the same or some other expression in the child

Cases are known in which the children of a dipsomaniac father and a quite normal mother have exhibited a tendency to alcoholism, insanity and the like In this case the possibility of poisoning the unborn child is eliminated, but there remain three possibilities of interpretation—that there was specific poisoning of the paternal germ cells that what was inherited was the constitutional weakness which expressed itself as alcoholism in the father and that there were detrimental influences in the early nutrition environment, education—nurture in short—of the offspring

But while we have admitted a good deal, we have not admitted the transmissibility of a particular structural modification brought about in the parental body as a result of the toxin

Misunderstanding VIII —*Failure to distinguish between the possible inheritance of a particular modification and the possible inheritance of indirect results of that modification or of changes correlated with*

it—At first sight this seems hair splitting but it is a crucial point. Through his vigorous exercise the blacksmith develops a muscular arm worthy of admiration, the shoemaker acquires skeletal and muscular peculiarities less admirable There are many permanent and profound modifications associated with particular occupations Are we to believe it is asked that the occupation of the parents has no influence on the offspring? Are we to believe it is asked that the children of soldier sailor tinker, tailor are in no way affected by the parental functions?

It would be interesting to have precise data in regard to this but it is generally admitted that when parents have healthful occupations their offspring are likely to be more vigorous The matter is complicated by the difficulty of estimating how much is due to good nurture before and after birth It is not unlikely too that some profound parental modifications may influence the general constitution may even affect the germ-cells and may thus have results in the offspring But unless the offspring show peculiarities *in the same direction* as the original modifications, we have no data bearing precisely on the question at issue

A belief in the inheritance of modifications was perhaps expressed in the old proverb The fathers have eaten sour grapes and the children s teeth are set on edge —a proverb which Ezekiel with such solemnity said was not any more to be used in Israel Now if setting on edge was a structural modification and if the children s teeth were set on edge as their fathers had been before them there would be a presumption in favour of the transmission of this acquired character though it would be still necessary to inquire carefully whether the children had not been in the vineyard too But if as Romanes said the children were born with wry necks we should have to deal with the inheritance of an indirect result of the parent s vagaries of appetite and not with any direct representation in inheritance of the particular modification produced in the paternal dentition

Misunderstanding IX —*Appealing to data from not more than two generations* —It has often been pointed out that animals transported to a new country or environment may exhibit some modification apparently the result of the novel influence and that their offspring in the same environment may exhibit the same modification *in a greater degree* Thus sheep may show a change in the character and length of their fleece and their progeny may show the same change more markedly

But it is perfectly clear that if the evidence does not go beyond this nothing is proved that affects the question at issue It was to be expected that the offspring should show the modification in a more marked degree than their parents did, since the offspring were subjected to the modifying influences from birth whereas their parents were influenced only from the date of their importation

What would be welcome is evidence that the *third* generation is more markedly modified than the second, then there would be data worth considering Only then would it be necessary to consider Weismann s somewhat subtle discussion as to the influence of climate

THE INHERITANCE OR NON INHERITANCE OF ACQUIRED CHARACTERS

EDWIN GRANT CONKLIN

Few questions in biology have been discussed so fully and so fruitlessly as this It is a problem of the greatest interest not only to students of biology but also to sociologists, educators and philanthropists and yet it is still to a certain extent an unsolved problem

Opinions of Lamarck and Darwin —It is well known that Lamarck taught that characters due to desire or need use or disuse, and to changed environment or conditions of life were inherited and thus brought about progressive evolution Long ago desire or need was repudiated as a factor of evolution Lowell satirized it in his *Biglow Papers* in these words

> Some filosifers think that a fakkilty s granted
> The minnit it s felt to be thoroughly wanted
>
> That the fears of a monkey whose holt chanced to fail
> Drawed the vertibry out to a prehensile tail [1]

Darwin wrote to Hooker Heaven forfend me from Lamarck s nonsense of adaptation from the slow willing of animals , but although he repudiated this feature of Lamarckism he held that characters due to use or disuse and to changed conditions of life might be inherited and he proposed his hypothesis of pangenesis in order to explain the process of the transmission of such characters to the germ cells

Weismann's theories —Weismann introduced a new era in biology by denying the inheritance of all kinds of acquired characters and by challenging the world to produce evidence that would stand a

From E. G Conklin *Heredity and Environment* (copyright 1919) Used by special permission of the publishers The Princeton University Press.

rigorous analysis But Weismann s greatest service lay in his con structive theories rather than in destructive criticism he forever disposed of theories of pangenesis and the like by showing that the germ cells are not built up by contributions from the body and that characters are not transmitted from generation to generation but on the other hand that there is transmitted a germ plasm which is relatively independent of the body and which is relatively very stable in organization This epoch making theory of Weismann s has natu rally undergone some changes as the result of new discoveries It is no longer believed that the germ plasm is really independent of the body, nor that it is absolutely stable as Weismann at one time held There is no doubt that the germ cells and the germ plasm are physiologically related to other cells and to other plasms and similarly there is no doubt that the germ plasm although very stable can and does change its constitution under some rare conditions But in the main the germ plasm theory is accepted by the great majority of biologists to-day and recent work in genetics and cytology has brought many confirmations of this theory

Distinctions between hereditary and acquired characters—As long as it was believed that the developed characters of an organism could be transmitted as such to its descendants it was customary to speak of developed characters as hereditary or acquired and to talk of the inheritance or non inheritance of acquired characters This dis tinction is not a logical one for all developed characters are invariably the result of the responses of the germinal organization to environ mental stimuli and of course no developed character can be purely hereditary or purely environmental But when a given character arises in many individuals of the same genotype under different environmental conditions it is probable that heredity which is the constant factor in this case is also the determining factor for that character On the other hand if a character develops in response to peculiar stimuli and does not appear in other individuals of the same genotype in which such stimuli are lacking it is said to be an environ mental or acquired character In fine inherited characters are those whose distinctive or differential causes are in the germ cells, while acquired characters are those whose differential causes are environ mental

Statement of problem.—Briefly stated the question of the inheri tance of acquired characters is this Can the differential cause of a character be shifted from the environment to the germ plasm? Can

peculiarities of the environment which influence the development of somatic characters so affect the germ cells that they will produce these somatic characters in the absence of the peculiar environment? Can the characteristics of a developed organism enter into its germ cells and be born again in the next generation? Considering the fact that germ cells are cells and contain no adult characteristics it seems very improbable that any peculiarity of environment whether of nutrition, use, disuse or injury, which brings about certain peculiarities of developed characters in the adult could so change the structure of the germ cells as to cause them to produce this same character in subsequent generations in the absence of its extrinsic cause How, for example, could defective nutrition which leads to the production of rickets, affect the germ cells which contain no bones, so as to produce rickets in subsequent generations although well nourished? Or how can over-exertion leading to hypertrophy of the heart so affect the germ cells that they, in turn would produce hypertrophied hearts in the absence of over-exertion seeing that germ cells have no hearts? Or how could the loss or injury of eyes or teeth or legs lead to the absence or weakened development of these organs in future generations seeing that inheritance must be through germ cells which possess none of these structures?

Lack of evidence for inheritance of acquired characters—But apart from these general objections to the doctrine of the inheritance of acquired characters there are many special difficulties There is no conclusive and satisfactory evidence in favor of such inheritance Almost all the evidence adduced serves to show only that characters are acquired not that they are inherited

It is a matter of common observation that mutilations are not inherited wooden legs do not run in families although wooden heads do The evidence for the inheritance of peculiarities due to use or disuse is wholly inconclusive, for example, did the giraffe get his long neck because he browsed on trees, or does he browse on trees because he has by inheritance a long neck? Did attempts to fly lead to the development of wings in birds or do birds fly because heredity has given them wings? Did life in caves make cave animals blind or did blind animals resort to caves because the struggle for existence there was less severe for them? The evidence is in favor of the second of each of these alternatives rather than of the first.

There still remains the question of the inheritance of certain characters due to environment, though here also the most clear-cut

evidence is against this proposition. That unusual conditions of food, temperature, moisture, etc., may affect the germ cells so as to produce general and indefinite variations in offspring is probable, but this is a very different thing from the inheritance of acquired characters. The germ cells being a part of the parental organism may be modified by such changes in the environment as affect the body as a whole; they may be well nourished or starved, they may be modified by changed conditions of gravity, salinity, pressure, temperature, etc.; and these modifications of the germ cells probably lead to certain general modifications of the adult, which may be larger or smaller, stronger or weaker, according as the germ is well or poorly nourished; but it is incredible that the environment which produces rickets or hypertrophied heart or loss of sight in one generation should modify the germ cells in such a peculiar and definite way that they should give rise in the next generation to these particular peculiarities in the absence of the extrinsic cause which first produced them. The inheritance of acquired characters is incredible because the egg is a cell and not an adult organism, and in this case there is no sufficient evidence that the thing which is incredible really does happen.

No inherited influence of stock on graft.—If specific changes of environment produced specific changes in heredity we should expect to find that where different plants or animals are grafted together each would modify more or less the hereditary constitution of the other. But this does not occur. Everybody knows that when a branch of a particular kind of fruit tree is grafted upon a tree of a different variety the quality of the fruit borne by that branch is not altered by its close union with the new stock. The same is true of all forms of animal grafts. Harrison cut in two young tadpoles of two species of frog, *Rana sylvatica* and *Rana palustris*, and spliced the anterior half of one to the posterior half of the other. These frogs and their tadpoles differ in color as well as in other respects, *R. sylvatica* being more deeply pigmented than *R. palustris*. In the grafted tadpoles each half preserved its own peculiarities even up to the adult condition.

A still more striking case of the persistence of heredity in spite of environmental changes is found in experiments in which the ovaries are removed from one variety of animal and transplanted to another variety. Guthrie made such transplantation in the case of fowls and concluded that there was some influence of the foster mother upon the transplanted ovary, but Davenport, who repeated his experiments, was unable to confirm his results. Finally Castle and Phillips furnished

the most conclusive demonstration that the hereditary characteristics of the transplanted ova are in no wise changed by the foster mother They removed the ovary from a pure black guinea pig and put it in the place of the ovary of a pure white animal After recovering from the operation this white female with the black ovary was bred to a pure white male Three litters of offspring from these parents were all pure black Although both parents were pure white all the offspring of the F1 generation were black because they came from black eggs and black is dominant over white The fact that these black eggs developed in the body of a white female did not in the least change their hereditary constitution

Dominants and recessives remain pure —A still more intimate union takes place when the dominant and recessive characters come together in any zygote These characters or rather the factors which determine them may be intimately associated in every cell of the organism throughout an entire generation and yet we may get a clean separation of these characters in the next generation in many cases neither the dominant nor the recessive character has been at all modified by its most intimate association with the other

Climatic effects not inherited —A striking instance of the purely temporary effect of the environment and of the long persistence of hereditary constitution amidst new environmental conditions which have greatly changed the appearance of the developed organisms is found in the case of alpine plants Nageli says that such plants which have preserved the characters of high mountain plants since the ice age lose these characters perfectly during their first summer in the lowlands

Summary —If acquired characters were really inherited we should expect to find many positive evidences of this instead of a few sporadic and doubtful cases In particular why do we not find in plant or animal grafting that the influence of the stock changes the hereditary potencies of the graft? Why do we not find that transplanted ovaries show the influence of the foster mother as Guthrie supposed—a thing which has been disproved by Castle? Why do dominant and recessive characters remain pure even after their intimate union in a hybrid so that pure dominants and pure recessives may be obtained in subsequent generations from this mixture? Why does every child have to learn anew what his parents learned so laboriously before him? Even the strongest defenders of the inheritance of acquired characters are constrained to admit that it occurs only sporadically and exceptionally

Neo-Lamarckism.—Many modifications of the Lamarckian hypothesis of the inheritance of acquired characters have been proposed in recent years. Foremost among those are the "mneme theory" of Semon and the "centro-epigenesis" theory of Rignano. To Semon as to many other biologists the apparent resemblance between memory and heredity has seemed significant and this furnishes the basis of his theory. Semon holds that every condition of life, every functional activity of an organism leaves a permanent record of itself in what he calls an "engramme." If these conditions or activities are long continued their engrammes are heaped up and affect heredity. Semon does not ask if "acquired characters" are inherited, but rather "Are the hereditary potencies of the germ cells altered by stimuli acting on the parental body?" This is a very different thing from the inheritance of a particular acquired character and there is some evidence that such stimuli may in rare instances produce changes in the hereditary constitution of the germ plasm though these evidences are by no means conclusive.

Temporary effects of environment: "induction."—On the other hand certain changes may be produced in germ cells or embryos which last for only a generation or two and then disappear. It is well known that plants grown in poor soil are smaller and produce smaller seeds than those grown in good soil, and De Vries, Bauer and Harris find that such seeds produce smaller plants having smaller seeds than do seed of normal size. This is an after effect of poor nutrition which changes the amount of food material in the seeds and through this the size of the plant which develops from the seed, but it does not change the hereditary constitution. Woltereck found that in *Daphnia* there is an after effect of cold lasting for one or two generations and this he calls "induction" when the effect lasts for one generation or "pre-induction" when it lasts for two or three generations. Whitney found that rotifers poisoned with alcohol were weaker in resistance to copper salts and were less fertile than others and when brought back to normal conditions the first generation was weak but the second was normal. On the other hand Stockard finds that the injurious effects of alcohol on guinea pigs persist through two or more generations. In man alcohol may have an "induction" effect on offspring but fortunately it does not seem to alter hereditary constitution. Probably of a similar character are Sumner's results; he found that mice raised in the cold have shorter tails than those raised in higher temperatures and this modified character appears in the next generation. If this is an after effect or "induction" it should disappear in the following generations.

Kammerer found that salamanders with black and yellow spots when reared on yellow soil gradually lose their black color becoming more yellow, and their young continue to grow more yellow until finally almost all black may disappear The offspring of such salamanders are said to be more yellow than normal but this work has been called in question and needs confirmation Even if confirmed the result may be an after effect or 'induction' which would soon disappear under usual conditions and there is no evidence that it is really inherited

Such cases are not instances of true inheritance, they do not signify a change in the hereditary constitution but an influence on the germ cell of a nutritive or chemical sort comparable with what takes place when fat stains are fed to animals the eggs of such animals are stained, and the young which develop from such eggs are also stained though the germinal constitution remains unchanged The very fact that the changed condition is reversible and that it disappears within a short time is evidence that it is not really inherited

In conclusion (1) Developed characters whether 'acquired' or not are never transmitted by heredity and the hereditary constitution of the germ is not changed by changes in such characters (2) Possibly environmental stimuli acting upon germ cells at an early stage in their development may rarely cause changes in hereditary constitution but changes produced in somatic cells do not cause corresponding changes in the hereditary constitution of the germ cells (3) Germ cells like somatic cells may undergo modifications which are not hereditary if starved they may produce stunted individuals and this effect may last for two or three generations they may be stained with fat stains and the generation to which they give rise be similarly stained, they may be poisoned with alcohol or modified by temperature and such influence be carried over to the next generation without becoming hereditary All such cases are known as 'induction and many instances of the supposed inheritance of acquired characters come under this category (4) Environment may profoundly modify individual development but it does not generally modify heredity

THE OTHER SIDE OF THE QUESTION

It will have been noted that the chief objection to the idea of the possibility of acquired characters being inherited comes to us as a heritage of the rather extreme Weismannian concept of the germ

plasm According to this view as brought out in another place (p 01) there is an unbroken continuity from generation to generation of the germ plasm Germ cells are thought of as remaining entirely undifferentiated for any somatic function and as therefore capable of starting at the beginning to develop a new individual The germ cell is supposed to be set apart at an early period in a given individual it takes no part in the formation of the individual s body, but remains a slumbering mass of potentialities which must bide its time to awaken into expression in a subsequent generation

Physiologists object to this idea that the germ cells are so distinctly different from body cells and that they are so insulated, as it were, from the soma as to be immune to any changes that may affec the latter Two kinds of data are offered in opposition to this con cept A few observers notably Professor C M Child have described cases in which somatic cells that already had become differentiated as primitive muscle cells, lost their differentiation and returned to a germinal condition If this kind of thing were general, and it is probably not germ cells might conceivably be produced from func tioning soma cells and might therefore furnish a mechanism for the transmission of the effects of use and disuse It should be empha sized however that among animals at least there is extremely little evidence in support of the idea that differentiated body cells give rise to germ cells

Among plants, however a different situation prevails In the *Begonia*, for example any part of a plant if cut off is capable of pro ducing a whole new plant Even a purely vegetative organ like a leaf if cut off and partially buried in soil will bud off a new plant which will produce flowers with perfectly typical germ cells We have to admit in this case either that leaf tissues contain undifferentiated germ cells or that somatic tissues give rise to germ cells The first alterna tive is in harmony with the germ plasm hypothesis the second is the preferred view of the opponents of this hypothesis

Among animals as for example annelid worms it is quite common to find the germ cells aggregated in a few egments of the body If a part of the body in which there are no recognizable germ cells be cut off it will under proper conditions regenerate the lost parts and become a complete worm with functional germ cells The same alternative explanations that were offered for the *Begonia* case apply equally well here Numerous other cases of the same sort are well known to all zoologists To the advocate of the germ plasm theory

they offer no difficulties because he can always fall back upon the statement that, among the lower forms at least, there is reserve germ plasm equally distributed over the whole body ready to differentiate into definite germ cells when needed. This type of appeal is abhorrent to the physiologist, and with some justification, for it really begs the question by assuming that any cell that is capable of forming germ cells belongs to the more or less sacred lineage of germ plasm.

If we confine the application of the germ plasm idea to the higher animals such as vertebrates and insects we would obviate these chief objections and the present writer would take the view that it is only among the upper ranges of highly specialized animals that the continuity of the germ plasm concept holds solidly.

Another chief objection to the germ plasm concept has to do with the supposed insulation or apartness of the term plasm. Physiologists have found that there is an extremely intimate correlation in function between practically all parts of a living organism. Many of the structures such as the rudimentary pituitary body, the thyroids the adrenal body and various other bodies whose function was long unknown have now been shown to exercise a profound effect on the development of the whole body. Since practically all tissues are known to affect at least some other tissues is it likely, the physiologist asks, that none of the other tissues affect the germinal tissues? The organism is to be viewed it is said not as a collection of independently functioning parts but as a single coherent unit. On this view no tissue can be thought of as beyond the influence of organic changes.

The classic argument of the Weismannians was that *we can conceive of no mechanism* by means of which somatic changes can be carried back into the germ cells and therefore *there is no such mechanism*. Now the fallacy of this argument is obvious, even if we could conceive of no suitable mechanism for this purpose this does not preclude the existence of such a mechanism. Moreover according to Professor Guyer, just such a mechanism actually exists as will be brought out in the following quotation from one of his recent publications.

A POSSIBLE MECHANISM FOR THE TRANSMISSION OF ACQUIRED CHARACTERS

MICHAEL F GUYER

Some selectionists glibly assert that new characters arise as the result of spontaneous changes in the germ. What is meant by this?

From M F Guyer "Immune Sera and Certain Biological Problems" *American Naturalist* Vol LV (1921)

Just what is a spontaneous change? No one has ever succeeded in telling us And we may suspect, though perhaps it is heresy to do so that it is a well sounding phrase that is the equivalent of the three words 'I don t know Unwilling to admit of the modifying influence of external agencies on the germ such theorists resort to the fiction of a spontaneous change Coleridge somewhere has said What s gray with age becomes religion ' We have toyed so long with this idea of germinal continuity and the invulnerability of the germ that it has become for some of us wellnigh sacrosanct Living matter is living matter wherever it may be found but when it happens to be in the germ-cells verily, this corruptible has put on incorruption and this mortal immortality !

Now no one to day qualified by his knowledge of embryology and genetics to the right of an opinion would I think deny that the new organism is in the main the expression of what was in the germ line rather than of what it got directly from the body of its parents but does this fact necessarily carry with it the implication that the germ is insusceptible to modification from without? Is not the serum of organisms with blood or lymph an excellent medium through which external influences may operate upon it? Is it not more reasonable to postulate the origination of germinal changes through some such mechanism as this than to attribute it to mysterious spontaneous changes ?

With such thoughts in mind I and my research associate Dr E A Smith set about making various tests Without attempting to tell you of our as yet unsuccessful attempts to secure cytolysins which will operate in the developmental stages of such periodically renewed structures as feathers or to weary you with the history of our various other failures—of which there are an abundance—I wish to speak briefly about certain antenatal effects we secured in rabbits by means of fowl serum sensitized against rabbit crystalline lens and of the fact that such induced defects may become heritable

The crystalline lens of the rabbit was selected as antigen and fowls as the source of the antibodies The lenses of newly killed rabbits were pulped thoroughly in a mortar and diluted with normal saline solution About four cubic centimeters of this emulsion was then injected intraperitoneally or intravenously into each of several fowls. Four or five weekly treatments with such lens-emulsions were given Then a week or ten days after the last injection the blood serum of one or more of the fowls was used for injection into pregnant rabbits The rabbits had been so bred as to have the young advanced to about

the tenth day of pregnancy, since from the tenth to the thirteenth day seems to be a particularly important period in the development of the lens It is then growing rapidly and becomes surrounded by a rich vascular network that later disappears From four to seven cubic centimeters of the sensitized fowl serum were injected intravenously into the pregnant rabbits at intervals of two or three days for from ten days to two weeks Several rabbits died from the treatment and many young were killed in utero Of sixty one surviving young from mothers thus treated, four had one or both eyes conspicuously defective and five others had eyes which were clearly abnormal It is possible that still others were more or less affected since we judged only by obvious visible effects We found later in some of the descendants of these individuals that rabbits which passed for normal during their earlier months subsequently manifested traces of defects in their lenses or in other parts of the eye

The commonest abnormality seen in both the original subjects and in their descendants was partial or complete opacity of the lens usually accompanied by reduction in size Other defects were cleft iris persistent hyaloid artery bluish or silvery color instead of the characteristic red of the albino eye microphthalmia and even almost complete disappearance of the eyeball Taking into account the method of embryological development however—the relation of lens optic cup and choroid fissure—the defects are probably all attributable to the early injury of the lens In some cases, both among originals and descendants an eye microphthalmic at birth may undergo further degeneration such as collapse of the ball and what appears to be a resorption as if some solvent were operating upon it The eyes of the mothers apparently remained unaffected This is probably due to the fact that the lens tissue of the adult rabbit is largely avascular and therefore did not come into contact with the injected antibodies

That the changes in the eyes of the fetuses resulted from the action of lens antibodies is indicated by the fact that in not one of the forty eight controls obtained from mothers which had been treated with unsensitized fowl serum or with fowl serum sensitized to rabbit tissue other than lens was there evidence of eye defects, and I may add that among the hundred or more young obtained later from mothers which were being experimented upon with various types of sera or protein extracts for other purposes not a single case of eye-defect has appeared

As already stated once the anomaly is secured it may be transmitted to subsequent generations through breeding So far we have succeeded in passing it to the eighth generation without any other than the original treatment *The imperfection, indeed tends to become* worse in succeeding generations and also to occur in a proportionately greater number of young Though not analyzed completely as to its exact mode of inheritance it has in general the characteristics of a Mendelian recessive Like such anomalies as brachydactyly or polydactyly in man the transmission is not infrequently of an irregular unilateral type sometimes only the right, at others only the left eye showing the defect In the later generations probably in some measure as the result of selective breeding there is an increasing number of young which have both eyes affected

To determine whether the reappearance of the defect was due merely to the passing on of antibodies or kindred substances from the blood stream of the mother, or to true inheritance we mated defective eyed males to normal females from strains of rabbits unrelated to our defective eyed stock The first generations produced in this way were invariably normal eyed but when females of this generation were mated to defective eyed males again we secured defective-eyed young after the manner of an extracted Mendelian recessive It is obvious that in such cases the abnormality could only have been conveyed through the germ cells of the male and that it is therefore an example of true inheritance Subsequent matings have shown that these young transmit the eye anomalies as effectively as do individuals of the original lines A new strain of defective eyed young established about the time our original paper went to press is also flourishing and as regards transmission of the defect seems to differ in no way from the earlier stock

But now let us inquire as to where all this leads Without entering into a discussion of just what serologically is taking place in the body or in the germ of fetuses borne by the lens treated mothers the point I wish to emphasize is that a certain specific effect has been produced and what is of greater moment once the condition is established it may be not merely transmitted but inherited Whether the lens of the uterine young is first changed and then in turn induces a change in the lens producing antecedents in the germ-cells of these young or whether the specific antibody simultaneously affects the eyes and the germ cells of the young is not clear In any event it is evident that there is some constitutional identity between the

substance of the mature organ in question and the material antecedents of such an organ as it exists in the germ

Biologically considered, the most significant fact is that specific antibodies can induce specific modifications in the germ cell. Whether these antibodies are transmitted from the mother's blood or engendered in that of the young would seem to be of secondary importance. It stands to reason that antibodies originated in an animal's own blood will modify germinal factors if corresponding antibodies introduced from without can accomplish this.

The whole question as to how important such a fact may be in contributing to an understanding of the causes of the germinal changes in organisms in general which lead to variation and evolution, hinges on the question of whether changes in an animal's tissue will induce the formation of antibodies or kindred active substances in its own body. We have been steadily accumulating evidence that such reactions do occur.

In our own laboratory for example after many attempts we have succeeded in securing a defective-eyed young rabbit from a mother of normal stock by injecting her repeatedly with pulped rabbit lens before and during pregnancy. Since the young rabbit in question has both eyes badly affected there can be no question that a rabbit can build antibodies against rabbit tissue which are as effective as those engendered in a foreign species such as the fowl. We have likewise found it relatively easy to secure spermatoxins by directly injecting rabbits both male and female with rabbit spermatozoa. Moreover a given male will develop antibodies against his own spermatozoa if he is injected intravenously with the latter.

We are also securing evidence that serologic reactions induced in the fetus through operations on the mother are not mere passive transmissions but may become actively participated in by the tissues of the fetus. For example female rabbits sensitized with typhoid vaccine followed by living typhoid germs may transmit to their young and even to their grand descendants the ability to agglutinate typhoid bacilli in serum diluted from 60 to 160 times. From the standpoint of heredity we have no reason so far for maintaining that this is anything but placental transmission though we are going to practice immunization generation after generation for a number of generations to determine if a truly hereditary immunity will be established. However facts have come to light which show that there is more concerned in the operation than a mere transfer of antibodies from mother to

fetus. For instance the blood of young shortly after birth may show a higher titer than that of the mother. Again after two or three months of development the young of certain of the sensitized mothers have shown a rather sudden rise in titer, much above that of the mothers. In such cases it would seem that some mechanism in the young rabbit itself is constructing antibodies which supplement those passively derived from the mother. Possibly in the process of development some organ important in such reactions just came into functioning. If this is true further experiments may throw some light on the perplexing question of the source or sources of the antibodies in an animal. After a few weeks in such cases the titer drops back again. In still another set of experiments we found that young from a sensitized mother when nursed by a normal untreated mother retained a fairly high titer for several months and even showed the rise of titer mentioned. On the other hand young of an untreated mother when nursed by a sensitized mother acquired a fairly high titer from the milk of the foster mother but lost it rapidly after weaning time. Thus there are evidently constitutional factors operative in the young which have acquired their immunity through the placenta which are absent in the young whose antibodies were conveyed through food.

That changes in the blood serum may be caused by changed conditions in the tissues is further attested by many facts. For example in pregnancy the newly forming placenta may set free cells or cell products which sometimes at least cause changes in the blood serum of the mother though the exact nature of these changes is in dispute. Romer, using the complement fixation technique found that the serum of adult human beings may possess antibodies for their own lens proteins. Bradley and Sansum employing anaphylactic reactions found that guinea pigs injected with guinea pig tissue proteins (liver heart muscle testicle kidney) develop immunity reactions. Again during the late war the type of toxic action to which anaphylactic shock conforms was found to exist after extensive injury of the soft tissues. It resulted apparently from the absorption of poisonous substances of tissue origin into the circulation. In fact various cells and tissues when injured liberate such poisons and even blood in clotting is known to acquire a transient toxicity of this type.

With facts such as these before us is it not a rational hypothesis to assume that changes in various parts of a body may on occasion influence the representatives of such parts in the germ-cells borne by that body? This appears all the more probable when we recall the

facts learned from a study of precipitins and of anaphylaxis that each species of animal has a thread of fundamental similarity underlying the proteins of all its tissues There is no reason to suppose that germinal tissue forms an exception. The further fact that homologous tissues, though existing in different species of animals possess similar chemical characteristics shows that to get an effect there need not be absolute chemical identity between the substance of such a tissue as the lens and the germinal constituents of which it is the expression. And if this is true for lens why not for other tissues?

The blood serum of any organism with blood thus affords a means of conveying the effects of changes in a parental organ to the germ cell which contains the antecedent of such an organ As long as there is little change in the somatic element its germinal correlative would presumably remain constant but any alternations of the soma which give rise to the formation of anti bodies or other active agents particularly if long continued might induce changes in the germ Such a hypothesis would seem to be plausible at least in accounting for degenerative changes such as the deterioration of eyes in such forms as the mole or in fact, in the formation of vestigial organs in general

On the other hand there is no reason to infer that changes induced in the blood serum may not also be instrumental in leading to progressive as well as regressive evolution If we may have germinally destructive constituents engendered in the blood there is no valid reason for supposing that we may not also have constructive ones When we learn more about what initiates and promotes growth in a part through exercise or what causes hypertrophy of an organ we may likewise find how corresponding germinal antecedents of that part may be enhanced. Until such time we shall probably remain in the dark regarding the mechanism of progressive germinal changes. As already indicated in the hormones and chalones we have a wonderful series of secretions normally circulating in the blood and maintaining general physiological equilibrium That reciprocal stimulations of various organs occur by this means is a well-established fact. Hypertrophy or atrophy of an endocrine gland may produce pronounced effects in the furthermost reaches of the body Again we may inquire is it reasonable to suppose that the germinal tissues will be inviolate to all this ebb and flow of chemical influence? Should we not expect specific reactions or selections here no less surely than in other tissues? Destruction of the pars buccalis of the hypophysis in the frog tadpole will cause profound alteration in other endocrine organs such as the

adrenals and thyroids will retard the growth rate render the entire organism albinous and produce in the individual pigment cells a condition of sustained contraction Shall we conclude that such a far reaching influence as this particularly in a developing organism will pass the germ cells by unscathed?

Similarly growth in man is known to be controlled by a pituitary secretion that is carried by the blood to the various organs The normal development of secondary sexual characters is determined by products from the testes or ovaries and the activities of the generative organs themselves are intimately associated with the functioning of the adrenal and other glands The periods of ovulation are inhibited by secretions from the corpus luteum lactation is incited by products of the corpus luteum the involuting uterus and the placenta the carbohydrate metabolism in the liver and even in the most distant muscles is profoundly influenced by substances formed in the pancreas the pancreas liver and intestinal glands are set to secreting through the stimulus of a product formed in the duodenal and jejunal mucosae And still others of such remarkable interrelations can be cited

Truly one may pronounce that social complex of reciprocating individuals termed cells which make up an organism members one of another And with all of these co operative activities of the various parts of the body it is inconceivable to me at least that the germ-cells bathed in the same fluid nourished with the same food stand wholly apart

May we not surmise then that as regards inheritance and evolution Lamarck was not wholly in error when he stressed the importance of use and disuse of a part, or of modifications due to environmental change in altering the course of the hereditary stream particularly if we conceive of these influences as being prolonged possibly over many generations? Have we not in the serological mechanism of the body of animals an adequate means for the incitement of the germinal changes which underly certain aspects of evolution?

RECENT EXPERIMENTS BELIEVED TO FAVOR THE LAMARCKIAN THEORY

Guyer and Smith, in continuation of their earlier program report that they have induced hereditary changes in the eyes of fetuses by a much simpler method than that described above By simply destroy

ing the lens of the living female rabbit by 'needling *in situ* anti lens serum has been produced in the blood of these animals This material was as effective in preventing the development of lenses in some of the fetuses of these mothers as was the material produced by more elaborate serological methods Also the effects seem to be inherited in the same way as in the former experiments It should be noted that Guyer is very cautious in his statements and makes no claim that his work demonstrates the inheritance of acquired characters He realizes that the same specific material that is supposed to inhibit the development of eye structures in the young fetus might readily at the same time exert a specific influence upon the genes or factors for eye structures in the primordial germ cells that live contemporaneously with the somatic structures Thus two generations might be affected simultaneously—a case of parallel induction

Every important experiment in science becomes the target of attack and the experiments of Guyer and Smith are no exception Bagg and Hanson and Little have performed some very interesting experiments on the effects of radium emanations and of X rays on mammalian germ cells and Stockard has used alcohol in the same way All of these workers show that eye defects especially lens defects, are found most commonly occurring sometimes in the entire absence of other observable defects It would seem, then that eye defects are far from being specific, and they may not be specific in the experiments of Guyer and Smith There is no question but that the eye is the most susceptible part of the organism and that eye defects can be induced in vertebrates by almost any kind of inhibiting agent It was only when Guyer used the lens material, however that he got lens defects for when he used sera developed from other tissues no effect upon the lens was noted But no effect upon any other tissue was noted, seeming to show that no effective antigens of any sort were formed It is impossible at the present writing to predict what will be the final bearing of Guyer's and Smith s very significant experiments upon the problem of the inheritance of acquired characters

Griffith and Detlefson have recently reported some experiments upon mice that at first seemed almost crucial for our problem Rats were reared for several months in cages placed upon rotating tables They became adapted to the rotating condition to such an extent that when the rotation was stopped they seemed upset, showing signs of nystagmus (dizziness) and other symptoms of a changed physiological condition Some of the young born outside the cages showed irregulari

ties in their gait and other signs of nystagmus. Moreover, the young of parents rotated to the left showed different effects from those of parents rotated to the right. The condition is said to have been inherited for several generations. Detlefson however noted that the whirled rats and their offspring showed frequent pathological sequelae such as discharges from the ears and is now inclined to wonder whether Griffith has not merely presented us with numerous specimens of some vertebral disease. The implication is that the disease once started might be passed on to future generations by infection. It is generally understood that Detlefson has been repeating these experiments upon the Wistar Institute standard white rats and that his results are so far negative.

And thus stands the problem today. It is no more settled than it was fifty years ago but most of us are growing to be a little pessimistic about the whole matter.

CHAPTER XXXII

OTHER POSSIBLE GUIDING FACTORS

Orthogenesis —Geneticists as a rule feel that natural selection is the only guiding factor needed to account for the adaptive features of evolution They are inclined to be skeptical about the definiteness of the pathways of change that have been so strongly emphasized by palaeontologists and others T H Morgan at one time expressed the view that most of the beautifully precise orthogenetic pedigrees such as that of the horse family for example might be made up by selecting only those fossil forms that fitted well into the progressive series and ignoring those that did not fit so well He showed that one could make out a very pretty phylogeny of the spear heads displayed in museums in which each type leads to another type and all are capable of arrangement into a few orthogenetic series Since such a series is merely an artificial arrangement without phylogenetic significance the same might also to some extent be true for the orthogenetic series of the palaeontologist Some geneticists are inclined to think that the evolution of the horse family for example had been much less definitely directed than it is commonly supposed to be In each period there existed numerous less progressive types and many aberrant species as well as those that seem to follow the more direct lines leading to the modern horses In other words much of the definiteness of direction is the result of focusing attention upon a few of the types that make a good series and ignoring the ones that are not in line This criticism is possibly too iconoclastic There surely is in the horse pedigree some definiteness of trend amidst a flux of indefiniteness Hence the problem of explaining this residual definiteness still remains

In recent years one of the staunch supporters of the reality of orthogenesis has been *H F Osborn* His most striking material perhaps, consists of the fossil pedigrees of the *Titanotheres* a group of extinct ungulates somewhat resembling the modern rhinoceros They appeared relatively early in the evolution of mammals, and attained giant proportions great abundance and wide distribution before becoming extinct at the close of the Oligocene period Though the titanotheres started as small creatures about the size of terriers they reached almost the dimensions of elephants near the close of their career One of

their outstanding peculiarities consists of a unique type of horn on the tip of the nose a horn branching at the base and diverging laterally into two flat prongs Osborn distinguishes at least four divergent lines of evolution among these mammals Line I retained the front teeth (incisors) and remained heavy bodied Line II lost the incisors and became longer limbed lighter bodied speedier and went in for grazing In neither of these lines did the horns grow very large Line III the first of the large horned lines lost the incisors and remained relatively small bodied Line IV to which the giant *Bro totherium* belongs retained the incisors grew extremely bulky and went in for slow leisurely browsing

In all these four lines that are known to have separated early and to have remained genetically independent throughout their careers the evolution of the horns has run parallel courses All four lines started hornless each developed horns independently and the steps in horn evolution ran the same course in all the four lines going some what farther in the larger types than in the smaller In the last sur viving representatives of all four lines the horns had reached the same characteristic form being attached to the same bones of the skull and having a shape quite unlike that known for any other group of mam mals

The inferences that have been drawn from this situation are as follows The original ancestral titanotheres must have had something in the germ plasm that was predestined to vary along certain definite lines and to produce certain definite structures in spite of any differ ences in environment or habits of the different lines of descendants The horns were compelled to appear at a certain stage in the evolution of each of the four lines though they may have had little or no adap tive value Osborn has no very satisfactory theory as to the mechan ism involved in this remarkable orthogenesis but Julian Huxley has offered a purely physiological explanation of horn evolution in titano theres an explanation that may apply equally well to many other cases He has discovered that in horned animals in general the larger the individual the larger are the horns in proportion to the body size Now as is true of most phylogenetic series there was a steady increase in size in all four lines of titanotheres Thus the earliest titanotheres were too small to have horns at all the first horned types were of moderate size the most elaborately horned types were the giant end products of each of the four lines, and especially was this the case for the great *Brontotherium*

If, then, as seems to be the case, horn evolution is merely a secondary and purely incidental consequence of increase in size, we may well ask why increase in size goes on so steadily? Is this not an orthogenetic process itself? But increase in size may be guided by natural selection without the aid of other factors, for increase in size confers a personal advantage upon the individual, though it may in the end be damaging to the race. Thus a larger bull in a herd will be stronger and win more mates, thus tending to pass on the genes for larger size to descendants.

Darwin would have called the case of horns in titanotheres an example of "correlated variation" and would have said that here we have an instance of some adaptive characteristic such as body size carrying along with it a variable character that may have little or no adaptive value. Thus this classic case of orthogenesis would be explained satisfactorily as the result of correlated variation and natural selection without dragging in any inner guiding principle.

In view of these and many other facts, it seems advisable, for the present at least, to say nothing further about orthogenesis. No very good case of orthogenesis has been presented that cannot be explained as well by natural selection as in any other way that has been suggested. So little do geneticists as a group think of orthogenesis as a possible guiding factor in evolution that most textbooks of genetics do not mention the word even in the index. Orthogenesis is at present a concept that belongs rather to the philosophy of evolution than to the science of genetics.

Vitalistic theories. — All theories of evolution based on known mechanisms are considered as mechanistic and belong in the realm of science, but there are some theories known as "vitalistic" that belong more to the realm of philosophy than to that of science. Several of these theories deal with some kind of immaterial force or forces that are believed to guide the course of evolution. Bergson's *élan vital* or "vital urge" is one of these immaterial forces. This force is believed to be practically synonymous with life itself. It is that property of life that gives to it a drive forward, a tendency to grow, multiply, and adapt itself. In a sense it is a sort of inarticulate purpose residing in the living substance itself. This protoplasmic purpose continually expresses itself in adaptive development and adaptive behavior. It realizes itself most completely as mind, purpose, and reason in higher organisms, but its essence is present in even the lowest organisms and in the youngest stages of the individual. It guides the course of in-

dividual development each step of which seems to be in preparation for the next, as though taken in anticipation of it

The reader may well revolt against the introduction of speculations of this sort into a treatment of the mechanism of evolution but if such a concept as *élan vital* does nothing more than to serve as a contrast with the more tangible and verifiable mechanisms of evolution we have previously dealt with it will have justified the space given to it

CHAPTER XXXIII

DIVIDING FACTORS: ISOLATION

Introductory. — As has so often been pointed out, one of the most conspicuous features of animal and plant life is their subdivision into a multiplicity of taxonomic divisions, such as phyla, classes, orders, families, genera, species and varieties. In any one particular environment one finds large numbers of representatives of numerous groups, a fact that seems to imply that the environment alone is an insufficient cause of multiplicity of forms; for if it were, a single environment should produce only one type and the same environment should always produce the same type. Also it is very frequently true that differences distinguishing two allied species are not obviously adapted to the differences in the environment, but are rather trivial characters such as color markings, proportions of parts, etc. Hence we cannot explain the multiplicity of types on purely environmental grounds.

Our studies of geographic distribution as evidences of evolution have emphasized the fact that mere geographic isolation, apart from climatic differences involved, are invariably accompanied by various degrees of divergence between the isolated members of the same group, the divergence sometimes being so great as to constitute family distinctions, more frequently generic, and very commonly specific or varietal. The degree of divergence parallels closely the degree of completeness of isolation and the extent of time during which isolation has been operative.

Opinions among authorities differ as to whether mutations and selection alone are sufficient to account for the multiplicity of forms and their distribution in space. Some of the more extreme neo-Darwinians, on the one hand, are inclined to believe that natural selection is sufficient unto itself to explain all of the observed facts. Extreme advocates of the isolation theory, on the other hand, look upon isolation as an absolutely essential mechanism for species formation nearly as important as natural selection itself. The writer believes that isolation is an absolutely essential part of any complete explanation of evolution, but that it is a subsidiary factor often working in such intimate relation with natural selection and Mendelian heredity as to be almost inseparable from them.

Isolation" used in the broadest sense —The term 'isolation is a somewhat unfortunate one to use for the type of factor we are here dealing with It implies physical separation in the geographical sense whereas there are very many types of isolation not at all based upon spatial separation In the broadest sense any factor may be said to play an isolating role if it interferes with free interbreeding among all the members of a species Completely free interbreeding within the entire range of a species would result sooner or later in an equal distribution among the individuals of the species of all viable hereditary changes Unless something were to interfere with free interbreeding within the species it would remain indefinitely one evolving unit and would not subdivide

But there are a great many ways in which free interbreeding may be interfered with Among the most important isolating agents are the following (a) geographic isolation involving the setting up of geographic barriers between subdivisions of the species (b) sheer distance apart of extreme sections of a species covering a large territory not involving any other isolation agencies (c) climatic differences within the range of the species (d) physical differences in the environment such as differences in water soil sunlight elevation of land etc (e) biotic differences in the environment involving the presence of various other animals and plants within the range of the species in question (f) reproductive differences among individuals due to genetic changes that alter the developmental rhythm or the copulatory apparatus bringing about assortative mating and (g) psychic differences that result in what is known as clannishness among human beings according to which changed forms tend to mate with their own kind more readily than with others

All these and doubtless other agencies promote isolation of small or large groups within the species and tend to split the species up into a number of more or less separately breeding groups

Isolation and inbreeding —One of the inevitable consequences of the isolation of a relatively small group from the main body of the species is inbreeding more or less close In extreme cases of geographic isolation a new race may be derived from one pair of individuals The offspring of such a pair if they breed at all must breed together and for successive generations there will be much close inbreeding Geneticists have demonstrated that continuous inbreeding results in a decrease of heterozygous and an increase in homozygous individuals Now even if no new mutations occurred nor any selection of types due

to changed environmental requirements took place such an isolated group would already have a good start toward becoming a separate race or species because of the effects of inbreeding

Isolation and selection—Divergence may also be promoted by selection When an isolated group of a species finds itself in a different environment from that of the parent stock selection may tend to preserve individuals with either the dominant or the recessive of any unit character or any combination of these that may happen to be more advantageous than others under the changed conditions of life In this way some genes may be entirely eliminated from a stock thus increasing the genetic differences between the parent species and their isolated derivatives If for example a small section of a species were to become isolated in a region where the available food was quite different from that in the main range of the species some of the individuals because of favorable combinations of unit characters might immediately find themselves better equipped to cope with the new food conditions than others Those adapted to the new food conditions would live and breed together and would tend to become homozygous for the various characters that favored their survival under the new conditions

THE VARIOUS CATEGORIES OF ISOLATION

a) **Geographic Isolation**—Taxonomists who have studied and plotted the distribution of species of animals and plants are most familiar with the effects of geographic isolation They consider that one of the most certain facts of nature is that isolation is always accompanied by marked differences between the isolated branches of a species The late *David Starr Jordan*[1] a leading student of geographic isolation in America discusses the subject in a very illuminating fashion

'It is now nearly forty years since Moritz Wagner (1868) first made it clear that geographic isolation (*räumliche Sonderung*) was a factor or condition in the formation of every species race or tribe of animal or plant we know on the face of the earth This conclusion is accepted as almost self evident by every competent student of species or of the geographical distribution of species But to those who approach the subject of evolution from some other side the principles set forth by Wagner seem less clear They have never been confuted scarcely ever attacked, so far as the present writer remem

[1] *Science* N S Vol XXII (1905)

bers but in the literature of evolution of the present day they have been almost universally ignored Nowadays much of our discussion turns on the question of whether or not minute favorable variations would enable their possessors little by little to gain on the parent stock so that a new race would be established side by side with the old or on whether a wide fluctuation or mutation would give rise to a new species which would hold its own in competition with the parent In theory either of these conditions might exist In fact both of them are virtually unknown In nature a closely related distinct species is not often quite side by side with the old It is simply next to it geographically or geologically speaking and the degree of distinction almost always bears a relation to the importance or the permanence of the barrier separating the supposed new stock from the parent stock

'A flood of light may be thrown on the theoretical problem of the origin of species by the study of the probable actual origin of species with which we are familiar or of which the actual history or the actual ramifications may in some degree be traced

In regions broken by few barriers migration and interbreeding being allowed we find widely distributed species homogeneous in their character the members showing individual fluctuation and climatic effects but remaining uniform in most regards all representatives slowly changing together in the process of adaptation by natural selection In regions broken by barriers which isolate groups of individuals we find a great number of related species though in most cases the same region contains a smaller number of genera or families In other words the new species will be formed conditioned on isolation though these same barriers may shut out altogether forms of life which would invade the open district

Given any species in any region the nearest related species is not likely to be found in the same region nor in a remote region but in a neighboring district separated from the first by a barrier of some sort

Doubtless wide fluctuations or mutations in every species are more common than we suppose With free access to the mass of the species these are lost through interbreeding Isolate them as in a garden or an enclosure or on an island and these may be continued and intensified to form new species or races Any horticulturist will illustrate this

In all these and in similar cases we may confidently affirm The adaptive characters a species may present are due to natural selection

or are developed in connection with the demands of competition The characters non adaptive which chiefly distinguish species do not result from natural selection but from some form of geographical isolation and the segregation of individuals resulting from it'

J T Gulick another exponent of the efficacy of geographic isolation in species forming has offered in evidence of his views facts about the distribution of Hawaiian land snails In the island of Oahu, for example the volcanic ridges have been eroded out into a series of isolated valleys in the bottoms of which grows abundant vegetation while on the highlands there is little but barren rock The climatic conditions of all the numerous valleys are the same but, remarkably enough each variety of snail is confined not only to one island but to a definite valley on an island The degree of difference moreover between varieties is in proportion to the distance that separates them Gulick claimed that he was able to estimate the degree of divergence between the snails of any two valleys by measuring the number of miles that lay between them Gulick s findings have been extensively corroborated by recent explorations on the snails of other oceanic islands by Crampton

An interesting type of isolation that hardly can be termed geographic yet i essentially equivalent to the latter in its effects is found in connection with the extensive group of lice (Mallophaga) that live their whole lives buried among the feathers of birds or the hair of mammals These animals cannot fly and are quite effectively isolated for life upon a particular bird They do however during the intimate period of nesting pass from parent to offspring, so that they may be said to be isolated upon definite genetic lines In the case especially of birds like the eagle a bird of long life and monogamous habits, the parasite becomes as isolated as might be a race on a small island The result is that sometimes the lice of a single bird and its offspring are of quite a distinct variety which has become fixed by inbreeding until a high degree of uniformity has been attained Such an isolated variety may be almost as distinct as a true species Obviously in this case as in others isolation must have had a real effect upon species forming quite apart from natural selection except in so far as the unfit variants have not survived

Populations of lakes and ponds—Just as islands of land in seas of water serve to isolate terrestrial forms so islands of water in seas of land if we may be pardoned the expression just as effectively isolate aquatic organisms Thus isolated ponds and lakes commonly harbor

species of fishes and other aquatic types different from those found anywhere else in the world As a young naturalist, I became interested in the fauna of Lake Maxinkuckee in Indiana a spring fed lake that is practically cut off from communication with other bodies of water While I was there Evermann and Clark were making a very exhaustive biological survey of this lake and discovered a surprising number of species peculiar to this one body of water Hundreds of similar situations doubtless exist all over the world

Populations of mountains —Certain types of plants characteristic of high mountains are commonly isolated from others of their kind by valleys and by discontinuities in mountain chains Patches of lowland thus isolate patches of mountains and the result is as one might expect that each isolated high mountain chain has its own local races or sub species of plants

b) Isolation due to sheer distance apart —If a species ranges all over a wide extent of territory which is unbroken by barriers there may be isolation because of the great distances between extreme outlying sections of the range Students of the evolution of great groups of mammals for example consider that very large continental bodies must have been the main theaters of evolution because smaller land bodies would not permit of diversification of types through isolation Thus the body of land known as Holarctica embodying Northern Asia Northern Europe and Northern America is believed to have been the principal theater of mammalian evolution In this great area there was plenty of room for groups to become spatially isolated even without positive barriers and in this area it is believed that all the original divergences occurred that gave origin to the princple subdivisions of mammals Migration along many southern routes has subsequently more completely isolated and fixed the various mammalian faunas of Southern Asia Australasia Africa, and South America

The original divergences resulting from mere spatial isolation would be the result of the inability of the most widely separated sections of a species to interbreed If they failed to interbreed mutations occurring in one section would remain in that section and those occurring in another section would likewise remain in that section Thus two independent evolutions would go on and local races or varieties would result that in time would become separate species especially if they subsequently migrated along different paths to different isolated regions

A good example of geographic races or sub-species arising in an extensive area unbroken by effective barriers is seen in the case of the wrens of South America. Wrens are found practically all over that continent, but those in one region differ from those in others in color patterns, size proportions and habits. In the absence of barriers all these local races grade into each other. In certain regions, however, that happen to be more than usually isolated, as when a high mountain range intervenes, transitional forms are missing. The point is, however, that whether barriers are present or not, sheer distance apart tends to produce local races.

c) Climatic isolation.—There often occur distinct and more or less abrupt climatic differences within the range of a species which may act as barriers to migration or involve different adaptive changes on the part of individuals living under these different climatic conditions. Thus, without the presence of any geographic barriers, a species may split up into a northern and a southern race or sub-species that are genetically distinct, neither thriving in the territory occupied by the other. Similarly, in the oceans there exist rather abrupt differences in temperatures that act as effective barriers. The waters north and south of Cape Cod, for example, have almost entirely different faunas. The reason for this is that the shore line north of Cape Cod is made cold by the Labrador Current and that south of the Cape is more influenced by the warm Gulf Stream. Species north of the Cape and south of the Cape are almost as distinct as if they belonged to different oceans.

d) Biotic isolation.—The territory occupied by any species of animal or plant is always occupied by many other species. Some of these associated species may occupy one part, some another part, of the range of the species in question. Now each species affects all the other species with which it is spatially associated; each species is a part of the biotic environment of all the others. If, then, the biotic environment varies within the range of the species, the pressure of selection will vary also, certain characters or combinations of characters being more favorable for one biotic environment than another. This being the case, groups in different biotic environments will tend to be isolated from one another and will diverge in both adaptive and non-adaptive directions.

e) Reproductive isolation.—The simplest type of reproductive isolation is one that involves changes due to mutations in the copulatory organs. In some insects, for example, the copulatory organs are con-

structed on the lock and key principle only a certain pattern of key fitting a certain pattern of lock Any change in the pattern of these organs prevents the members of the changed type from breeding with the unchanged individuals and forces them to breed only with those that have changed in appropriate fashion Fortunately when a change occurs it usually affects both sexes in such a manner that males and females of the changed type can mate No actual observations of new races arising in this way have been observed but there are numerous cases of closely allied species that are intersterile because of slight differences in the pattern of their copulatory organs

One of the most effective means of bringing about reproductive isolation is a change in the developmental rhythm of a section of a species If for example some plants of a species flower earlier or later in the season than others they are able to interbreed only with those having the same developmental rate If such a difference in developmental rate be genetic a real isolation of these different races will be effected and further divergence will follow A similar situation also occurs among animals The genus *Cicada* commonly called locusts has probably split up into numerous species as the result of genetic modifications in the lengths of their life cycles Whereas there are only slight morphological differences among the species of *Cicada* there are pronounced differences in the lengths of the larval periods In the seventeen year locusts for example the larval life under ground is over sixteen years As a result of this only once in seventeen years do the adult broods appear above ground They must therefore mate only with members of their own brood in the same territory Similarly there are fourteen year eleven year nine year and seven year species etc each of which is reproductively isolated in any territory from all others for rarely do two species reach maturity in any region during the same season Even in one species scattered over a wide expanse of territory different broods appear one or two seasons apart and this tends to isolate sections of the present species from one another and will doubtless produce further splitting up of species as time goes on Doubtless many other situations similar to these but less extreme exist among both animals and plants That changes in developmental rate do exist within a species and have a genetic basis is attested by the fact that many early and late fruiting varieties of domestic plants have been isolated some of which are more suitable for a long southern growing season and others for the relatively short northern season

f) Psychic isolation —A synonym for psychic isolation is "clannishness" Even among lower animals there appears to be a well defined tendency for like to mate with like Assortative mating is another term commonly used to denote this tendency In man conventional mating is highly assortative Sporadic sex unions between members of radically different races not uncommonly occur but formal marriages are rare between members of distinct races. This tends to preserve a residue of racial separateness that would long ago have disappeared except for clannishness

Examples of this sort of thing in the animal world are not far to seek *Beebe* cites the interesting case of two color phases of gannets occupying an old volcanic crater together but keeping absolutely separate in their breeding activities The main gannet population consisted of white birds but out toward the center of the crater there was a small compact and unmixed clump of sooty birds which could doubtless have readily interbred with whites but never did so preferring their own kind

It was Darwin I believe who described the case of droves of wild horses of the Caucasus region that were all of one color in a drove One drove would be all bays another all blacks another all chestnuts Apparently these droves consisted of closely related individuals that preferred to mate only with their own kind Long-continued reproductive isolation of this sort might readily bring about the origin of separate races and in time separate species

Most of the types of isolation briefly discussed above are somewhat hypothetical in that they are derived from observations of nature "after the event" as it were Very little real experimental work has been done in this field except in connection with inbreeding and selection In animal and plant breeding man merely isolates a pair of individuals usually beginning with a brother and sister, and begins an inbred line, selecting usually the most promising individuals for further inbreeding In this way excellent homozygous strains are produced that have peculiar characteristics of their own unlike those of any other strain Hence, artificial inbreeding and selection is a kind of reproductive isolation having the same effects as has extreme isolation in nature There can be no doubt, then, that the various types of isolation have the effects attributed to them, namely those of splitting up species and of preserving incipient races from being swamped out by back crossing with the parent stock

PART IV

EUGENICS

CHAPTER XXXIV

INTRODUCTION TO EUGENICS

Definitions of eugenics.—"Eugenics" is a term coined by Sir Francis Galton in 1883 and was defined by him as the "study of agencies under social control that may improve or impair the racial qualities of future generations either physically or mentally." More specifically, eugenics is that science which deals with human variation and heredity and attempts to improve the human stock by selective breeding according to the known laws of genetics. In still different words, eugenics may be defined as the application of genetics to man with the hope that man might control his own evolution and save himself from racial degeneration.

Eugenists feel that many of the ills of the world might be cured by an application of eugenic measures. "We must endeavor," says a president of the American Eugenic Society, "to show that eugenics supplies the most effective and permanent solution to the problems that have been so ineffectively dealt with hitherto by physicians, public health officials, social workers, clergymen and reformers—the problems of combating disease, disability, defectiveness, degeneracy, delinquency, vice and crime."

This rather sanguine statement is echoed in somewhat different words by Jennings: "The troubles of the world and the remedy of these troubles lie fundamentally in the diverse hereditary constitutions of human beings. Some men are strong, healthy, wise, virtuous. Others are weak, foolish, diseased, immoral, criminal, and it is these that cause the troubles of the world. Laws, customs, education, material surroundings are the creations of men and reflect their fundamental nature. To attempt to correct these things is merely to treat superficial symptoms. To go to the root of the troubles a better breed of men must be produced, one that shall not contain the inferior types. When a better breed has taken over the business of the world, laws, customs, education, material conditions will take care of themselves. Good men, wise men, will make a good world."

In a somewhat roundabout way we have thus defined eugenics by stating the views of some of the leading advocates of eugenics.

The scope of eugenics —The range of subjects usually considered within the realm of interest of students of eugenics may well be stated by quoting from the prospectus published in connection with the Second International Congress of Eugenics that met in New York in September, 1921 The Congress met in four sections each of which devoted itself to one of the major fields of eugenics The four sections are described as follows

"I. In the first section of the Congress will be presented on the one hand the results of research in the domain of pure genetics in animals and plants and on the other studies of *human heredity* The application to man of the laws of heredity and the physiology of reproduction as worked out on some of the lower animals will also be presented

"II The second section will consider factors which influence the *human family* and their control, the relation of fecundity of different strains and families and the question of social and legal control of such fecundity also the differential mortality of the eugenically superior and inferior stocks and the influence upon such mortality of special factors, such as war and epidemic and endemic diseases First in importance among the agencies for the improvement of the race is the marriage relation with its antecedent mate selection Such selection should be influenced by natural sentiment and by a knowledge of the significant family traits of the proposed consorts and of the method of inheritance of these traits In this connection will be brought forward facts of improved and of unimproved families and of the persistence, generation after generation of the best as well as the worst characteristics

"III The third section will concern itself with the topic of *human racial* differences with the sharp distinction between racial characteristics and the unnatural associations often created by political and national boundaries In this connection will be considered the facts of the migrations of races the influence of racial characteristics on human history, the teachings of the past with bearings on the policies of the future Certain prejudices directed toward existing races will be removed when allowance is made for the influence of their social and educational environment, and their fundamentally sound and strong racial characteristics are brought to light On the other hand limits to development of certain races and the inalterability through education and environment of the fundamental characteristics of certain stocks will be considered Finally the advantages and disadvantages

of the mingling of races of unions which have proved to be fateful to social progress should be discussed In this section will be presented the results of researches upon racial mixtures in relation to human history Also the topics of racial differences in disease and psychology will be taken up The history of race migrations and their influence on the fate of nations especially modern immigration should be set forth

IV The fourth section will discuss eugenics in relation to the state to society and to education It will include studies on certain practical applications of eugenic research and on the value of such findings to morals to education to history and to the various social problems and movements of the day In this section will be considered the bearing of genetical discoveries upon the question of human differences and upon the desirability of adjusting the educational program to such differences Here will be considered the importance of family history studies for the better understanding and treatment of various types of hospital cases and those requiring custodial care The bearings of genetics on sociology economics and the fate of nations may be considered in this section

This outline of the program of the Eugenics Congress shows clearly that eugenics is a broadly conceived subject It is not merely a branch of genetics but has intimate relations with sociology economics legal science political science the scientific study of crime and delinquency medical science and education

The aims and ideals of eugenics —The hopes and ideals of eugenists are well expressed in the closing paragraph of the address of the president of the last International Congress of Eugenics Major Leonard Darwin an illustrious grandson of Charles Darwin

Eugenics aims at increasing the rate of multiplication of stocks above the average in heritable qualities and at decreasing that rate in the case of stocks below that average But if the banner under which we are to fight should only have inscribed on it some such arid definition of policy as this our defeat would be certain We must prove that we are under the guidance of a noble ideal We of this generation are responsible for the production of the next generation and therefore of all mankind in the future and all in whom this sense of racial responsibility acts as a deep-seated sentiment greatly affecting their action and their policy are in truth guided by the eugenic ideal. The belief that man has been slowly developed from some ape like progenitor came toward the close of the last century to be near

ly universally held by thoughtful persons this belief gave rise to a new hope that this upward march of mankind might be continued in the future, and out of this new hope sprang the eugenic ideal This growing understanding of the past history of the world has led us to see that, if we are to imitate Nature in her methods we must be content to advance by a long succession of small steps just as rain falling in drops on the earth has slowly carved out mighty valleys in the hardest rocks Without constructing wild Utopias we must be content if some little racial progress can be ensured as each generation succeeds another for to work in this spirit is to work in harmony with the knowledge which gave birth to the eugenic ideal Progress on eugenic lines will make mankind continually nobler happier and healthier, whilst those who imagine that our sole aim is to make man a stronger animal or a better beast of burden are utterly ignorant of the meaning of the eugenic ideal But science whilst giving us good grounds for hope also issues a grave warning concerning the danger of national deterioration resulting from the unchecked multiplication of inferior types In the past many nations of the first rank when apparently advancing without check on the path of prosperity, have begun to decay from unseen causes and have in time so fallen from their high estate as to cease to count as factors making for progress A determination that such a downfall shall not be the fate of his nation is a sentiment felt by every man who is animated by the eugenic ideal an ideal to be followed like a flag in battle without thought of personal gain

Methods of research in eugenics —The programs of research in the field of eugenics as broadly stated in the four paragraphs outlining the four sections of the Congress cover so many interests and impinge upon so many fields of research that have little if any bearing on the subject matter of the present course that we shall limit our discussion of methods to those applicable to the study of human heredity The chief methods of discovering the facts about human heredity are as follows

a) The pedigree method —According to this method a study is made of the history of human matings including all generations simultaneously living and the records of those recently deceased The method of the experimental breeder cannot be used but each fertile human mating is looked upon as an experiment in genetics, the results of which we may record and from which we may draw conclusions

b) *The statistical method* —A great deal can be learned about the heredity of fluctuating and graduated differences such as those of height weight, longevity etc by determining the degree of correlation that exists between a large group of parents and a large group of offspring Galton and his successor Karl Pearson are the chief exponents of this method

c) *The twin method* —This method is quite distinct from either of those just listed though it may use statistical methods Many facts may be determined by the use of one egg (monozygotic) and two-egg (dizygotic) twins about what is inherited in man and what characters are commonly modified by the environment

A separate chapter will be devoted to a discussion of each of these methods and the contributions to our knowledge of human heredity that have accrued from their use

CHAPTER XXXV

HUMAN HEREDITY AS REVEALED BY PEDIGREES

Weaknesses of the pedigree method.—The older type of pedigree study involved the collecting of pedigrees made out by persons untrained in genetics and dealing with individuals in their own family connections. Questionnaires were sent out to large numbers of individuals asking them to give data as to characteristics of their ancestors and other relatives. Much of the material thus collected depended upon the vague memories of individuals about the characteristics of long dead ancestors or of relatives in collateral lines. The low degree of reliability of such data makes conclusions therefrom almost useless. Considerably more reliable data were obtained by field workers who actually observed individuals belonging to four, in extreme cases five generations all living simultaneously. The reliability of such data depends upon the training and scientific aptitude of the field worker. Fortunately there has developed in recent years a new profession, that of eugenic field worker, and there are not a few very capable persons belonging to this profession. Another weakness of the pedigree method is that it affords no check on the actual parentage of offspring. The mother is usually not in doubt, but there is often some question as to the actual father. This is principally true in connection with the study of pedigrees of feeble minded and delinquent stocks and of primitive peoples with moral codes somewhat less rigid than our own. In other words, the genetic data acquired by this method are not scientifically controlled. Still another weakness of this method is that it is not always possible to distinguish between conditions that are hereditary and those due to disease or poor environment. In spite of these weaknesses, the pedigree method has brought to light a great deal of valuable information about human heredity. So long as one retains a properly critical attitude toward data and conclusions, no harm and much good may accrue from a review of the principal results of this method of research.

Two postulates underlying the study of the heredity of human traits may be set down as follows: (1) When characters are inherited according to the laws of Mendel, that is, when one of a pair of characters is dominant, or partly so, and the other recessive, and they segre-

gate in Mendelian ratios in subsequent generations such character differences are determined by genes (2) Allelomorphic differences have arisen through the process of gene mutation a process so well established for lower organisms These postulates are justified for it is hardly likely that so universal a method of heredity as the Mendelian method operates for the rest of the organic world and not for man Also the method of gene mutation is the only method by means of which allelomorphic differences are yet known to arise and it is hardly likely that man is an exception to the rule

The rate of mutation for man has been worked out for various races of mankind The number is almost the same in the various races For every 115 normal genes in the Russian race there are about 5 more mutant genes than in the Negro race If 6 000 generations says Danforth represents anywhere nearly the time since these two groups along with others diverged from a common ancestor these additional mutant genes must have been acquired in this length of time These figures indicate that in the course of 6 000 generations at least 5 in every 115 gene lines which have persisted underwent mutation in this one direction Since there is no evidence of selection this may be presumed to be the rate of mutation in this particular germplasm from which it follows that there has been on the average one mutation in every generation for each 138 000 genes If as some might be inclined to think the two germplasms have passed through more than 6 000 generations since they separated the rate of mutation has been less than this

Thus we see that mutations though infrequent continue to appear at a slow and steady rate Like the mutations in *Drosophila* and those of other animals studied the majority of mutations in man are poor many are indifferent and very few are good It has evidently taken a long time for man to acquire the better hereditary traits he now possesses In the past natural election has tended to eliminate most of the undesirable mutants especially the dominant ones, but under civilized conditions mankind has done much to nullify the good work of natural selection by doing everything in his power to preserve the poorer mutants and help them to multiply

SOME HEREDITARY TRAITS IN MAN

Studies of nearly 200 human traits have been made In the majority of cases they can be classified as dominants ordinary recessives and sex linked recessives The latter are the easiest to detect for

they follow the familiar mode of heredity described for sex linked characters in *Drosophila*. Dominants may fairly readily be distinguished by the fact that at least one of the parents, one grandparent, one great grandparent, etc. exhibit the character; a dominant character appears in every generation. Ordinary autosomic, or non sex linked recessives are characterized by the irregularity of their incidence in pedigrees. They may skip one or several generations and only appear at all when the same recessive gene is present in the germ plasm of two mating individuals, in which case it will appear in the following ratios according to the genetic make-up of the parents: (*a*) If both are heterozygous, three out of four offspring will show the dominant and one the recessive character; (*b*) if one is a heterozygote and one a recessive, the offspring will be half heterozygous dominants and half recessives. Thus we see that recessive characters may be hidden for a long time awaiting a favorable mating to give them expression.

Most of the best pedigrees of human characters deal with relatively rare and atypical or abnormal characters; in fact, most of them deal with what we ordinarily call freaks or pathological conditions. The reason for this is that rare and unusual conditions are much more easily detected and recognized. Ordinary, common differences are hard to detect and hard to distinguish and therefore difficult to follow in pedigrees.

It is not our intention in this chapter to attempt an exhaustive treatment of the facts of heredity ascertained by the pedigree method. We shall merely list some of the commonest cases of hereditary characters and give a few pedigrees illustrating them.

The following is a list of human unit characters classed as dominants, ordinary recessives, and sex linked recessives.

A. DOMINANT CHARACTERS

Skin and Hair	
Dark skin	Dominant over blond or albino (probably due to two or more pairs of genes)
Spotted with white	Dominant over uniformly colored
Tylosis and ichthyosis	Thickened or scaly skin
Epidermolysis	Excessive blisters of skin
Brown or black hair	Dominant over red and flaxen (probably due to more than one gene)
Red hair	Dominant over flaxen
Beaded hair	Single hairs are not uniform in diameter

White forelock	White patch of hair in front
Hypotrychosis	Hairlessness associated with lack of teeth
Pattern baldness	Partly sex limited
Eyes	
Front of iris pigmented (eyes black brown hazel etc.)	Dominant over lack of pigment in front of iris (blue eyes)
Hereditary cataract	Opacity of lens
Night blindness when not sex linked	Inability to see in dim light
Displaced lens	Causing defective vision
Glaucoma	Swelling of eyeball due to internal pressure
Coloboma	Open suture of the iris
Pigmentary degeneration of retina	Causing blindness
Skeleton and Muscles	
Brachydactyly	Digits lacking one joint
Polydactyly	Extra digits
Syndactyly	Fused or webbed digits
Symphalangy	Fused joints of digits stiff fingers
Split hand	Palm cleft to the wrist
Lobster claw	No digits but thumb
Exostoses	Abnormal outgrowths of long bones
Brittle bones	Bones very fragile
Absence of palmaris longus muscle	Lack of a certain muscle in palm of hand
Muscular atrophy	Partially dominant
Body Build	
Achondroplasy	Dwarfs with short, stout limbs normal body and head
Short stature	Partly dominant over tallness
Obesity not due to glandular defects	Partially dominant
Nervous System and Kidneys	
Huntington s chorea	A type of St Vitus dance
Diabetes insipidus	Partially dominant
Diabetes mellitus	Partially dominant

B AUTOSOMIC RECESSIVE CHARACTERS

Albinism	Lack in pigment in skin and hair—sometimes pink eyes
Ateleosis	True dwarf body small with parts in normal proportions
Cretinism	Dwarfism due to hereditary thyroid deficiency

Alkaptonuria	Urine dark after oxidation
Otoschlerosis	Thickening of ear-drum
Left handedness	Probably recessive
Tendency to twinning	Probably recessive
Susceptibility to tuberculosis	Probably recessive
Thomsen's disease	Lack of muscular tone
Menier's disease	Dizziness and roaring in ears
Deaf mutism	Congenital deafness
Friedereick's disease	Degeneration of the upper part of the spinal cord
Multiple schlerosis	Diffuse degeneration of nervous tissue
Chorea	Ordinary St Vitus dance
Hereditary feeble mindedness	Probably recessive
Hereditary epilepsy	Probably recessive
Manic depressive insanity	Probably recessive
Dementia praecox	Probably recessive

C CHARACTERS DUE TO CUMULATIVE FACTORS

It is suspected that a good many of the characters listed as incompletely dominant may be due to cumulative factors producing the condition usually called blending heredity Those that almost certainly belong to this category are stature body weight (except certain types of obesity) skin color shape of head and proportions of features

D SEX LINKED RECESSIVES

Color blindness	Lack of discrimination between red and green
Night blindness	One form of this defect which involves inability to see in dim light
Haemophilia	Free bleeding
Gower's disease	Muscular atrophy
Neuritis optica	Progressive atrophy of the optic nerve

Some pedigrees of dominant characters—Perhaps the best example of a dominant trait that has been thoroughly worked out is *brachydactyly* a type of hand in which one joint is lacking in each digit In the normal hand the thumb has one less joint than the fingers Hence in a brachydactylous person all the fingers are thumbs and the thumb is a subthumb Such a type of hand is broad thick and clumsy It is not at all a well adapted character but it is not so bad but that it can survive Drinkwater has studied a number of brachydactylous pedigrees one of which is shown in Figure 81 Males in this chart are shown by ♂ and females by ♀ solid circles indicate affected

and open circles unaffected individuals Notice that the character appears in at least one parent in each generation which is characteris

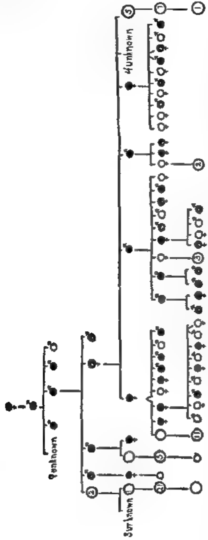


FIG 82 —Pedigree of a line with brachydactyly condensed and modified from Drinkwater's chart It reads thus A brachydactylous woman has a son also brachydactylous He has thirteen children the condition of nine of whom is unknown three possess the character one is normal One of these four known ones himself brachydactylous has six children The sex of two is not known but they were not brachydactylous three sons and one daughter were And so the family continues One sees at a glance how the defect continues generation after generation not reappearing however in the offspring of those who are free from it (*From Downing*)

tic of the mode of inheritance of dominant characters Also the number of individuals affected is about what one would expect in the case of a dominant character

The question arises with reference to this as well as to many other, dominant characters as to why being dominant the character does not become more prevalent rather than remaining relatively rare The answer that seems most probable is that the brachydactylous hand is very poorly adapted to human uses and those individuals possessing it are seriously handicapped Hence there may be marriage selection against it If it were more advantageous than the normal, doubtless the incidence of the character would increase and it might in time become the typical condition for the species ? The same explanation would apply equally well to all other cases of dominant abnormal

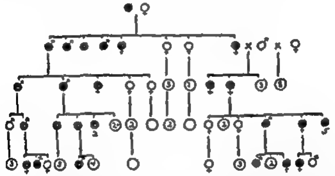


FIG 82 — Inheritance of one form of cataract Modified from Nettleship s chart The diagram reads thus A man with cataract married a normal woman of their eight children six were affected with the disease One of these married an unaffected man three of the children of this union were normal sex unrecorded two defective This same man married a second wife who was normal their eight children were all unaffected So continue reading through five generations (*From Downing*)

Mendelian traits It might also be asked why all the offspring of a dominant parent do not show the character The reason should be obvious namely that most individuals are heterozygous for the character A heterozygote mating with a recessive is expected to produce one half heterozygotes and one half recessives which is about what the accompanying pedigree shows

Another case of a dominant character not so definitely analyzed as the last is a type of *hereditary cataract* (Fig 82) This condition is due to an opaque region in the lens of the eye which when well advanced may cause blindness In the particular form of the disease here considered, ' says Downing ' it does not develop until middle life

Clarence Loeb in a study of hereditary blindness tabulated the results of 304 families in which such blindness occurs There were 1 012 children of whom 58 per cent were afflicted which is about the percentage expected when hybrid defectives mate with normal individuals and the defect is a dominant character

A typical pedigree of a recessive character—A good example of the mode of inheritance of an uncommon recessive character is shown in Figure 83 the pedigree of a family line showing outcropping of *albinism* lack of pigment in hair skin and eyes It is noteworthy that the appearance of the character is relatively rare only 19 out of 158 individuals in the pedigree being albinos or partial albinos that albino offspring are produced by two phenotypically normal (pigmented) parents, and that in generation VII where several of the children are albinos the two parents are descended from common ancestors a few generations back and are undoubtedly both heterozygous In this pedigree there are no cases of the mating of two albinos If such matings had occurred the expectation of course would be that all offspring would be albinos Since we shall have to present further examples of pedigrees of recessive characters in connection with the account of the heredity of mental characters we need give no further examples here

It is also unnecessary to repeat in this place the description of such sex linked human characters as color blindness haemophilia etc The accompanying chart (Fig 84) which represents an investigation of a Texas family connection made by the writer in 1910 is typical for sex linked characters The existence of sex linked heredity in man goes far to support the contention of eugenists that heredity in man follows the same rules as have been found to hold for the lower animals

As an example of human characters probably determined by *cumulative factors* we may cite the case of skin color Whole races of man are dark skinned others light skinned Some idea as to the mode of heredity of skin color is obtained by studies of crosses between negro and white individuals In a cross between a negro and a white person says Castle children are produced that are of an intermediate but frequently variable skin color and are known as mulattoes Mulattoes mating inter se produce an F generation of highly variable skin color but rarely pure white Davenport has concluded that two independent Mendelian factors affecting skin color are involved This explanation would lead us to expect one in sixteen of the F mulatto offspring to have skin as white as an European even though his negro

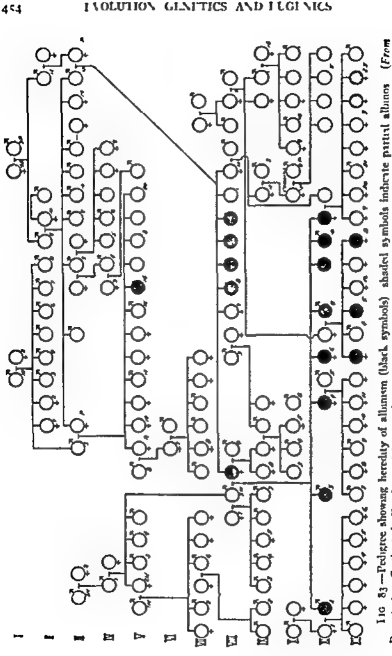


FIG 83 —Pedigree showing heredity of albinism (black symbols) shaded symbols indicate partial albinos (*From Davenport in Castle et al Heredity and Eugenics*)

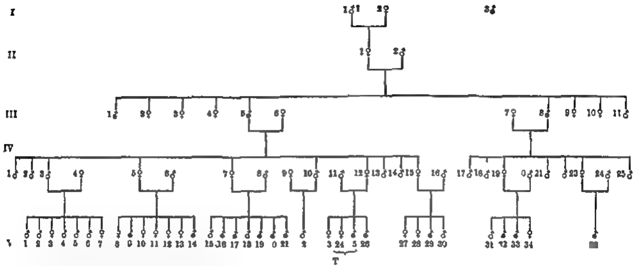


Fig 84 —A pedigree of five generations of a family showing sex linked night blindness (inability to see in dim light) Black symbols indicate those affected Note that all those affected are males (*From Newman*)

ancestry might show in other characteristics, such as curly hair, broad nose, thick lips, etc. It is difficult to get any wholly satisfactory evidence either for or against this explanation. That published by Davenport can scarcely be considered conclusive, for the data studied are derived from a population in which illegitimacy, by Davenport's own statement, is as high as 72 per cent. On the whole, it seems probable that segregation of skin pigmentation in mulattoes is either incomplete or rarely complete, because multiple or modifying factors are involved."

Having given examples of pedigrees of physical characters exhibiting all of the principal modes of Mendelian heredity, let us now pass to a consideration of the facts about the heredity of mental traits in man as revealed by pedigree studies.

HEREDITY OF MENTAL TRAITS IN MAN

The studies of the heredity of mental traits in man consist principally of those of exceptional genius and of definite mental defects and abnormalities. Very little effort has been expended upon the heredity of normal average intelligence, such as the great majority of us possess.

Long ago, in 1869, Sir Francis Galton published a fascinating book on *The Heredity of Genius*, in which he presented a large number of pedigrees of families showing definite and special types of genius, such as musical genius, genius for astronomy and mathematics, genius for science, etc. Among those described in some detail are the Bach family of great musicians in Germany, the Herschell family of great astronomers in England, and he might have added his own pedigree composed of the interrelated families of Darwins, Galtons, and Wedgewoods, the present generation of which consists of many outstanding and influential persons (Fig. 85). No family today shows more plainly than this one what can be done in the way of racial improvement through a certain amount of concentration of good germ plasm by judicious inbreeding (cousin marriages), when the inbreeding stocks are strong and sound. Charles Darwin, the most eminent member of this family connection, was the son of an eminent physician, a member of the Royal Society. One of Darwin's grandfathers was the well known Erasmus Darwin, referred to in the *History of Evolution* (chap. II). The other grandfather was Josiah Wedgewood, F.R.S., founder of the Wedgewood potteries. Charles Darwin married his own cousin, Emma Wedgewood. Four of Darwin's sons are eminent members of

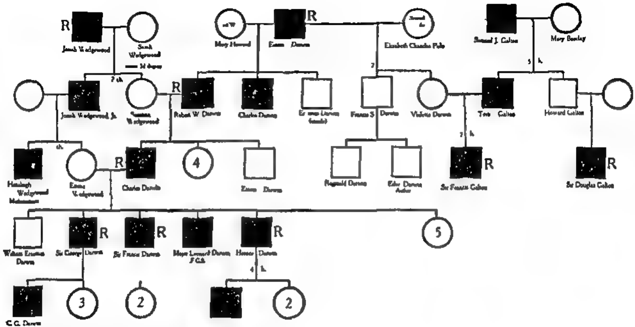


Fig 85.—Pedigree of the Darwin Galton Wedgewood Family Males of note black squares an *R* beside square denotes membership in the Royal Society Figures in circles show number of daughters if more than one

the Royal Society one of them being Major Leonard Darwin, president of the Second International Congress of Eugenics from whose speech we quoted a paragraph in the previous chapter Darwin s aunt married into the famous Galton family and her son was the late Sir Francis Galton the originator of the term "eugenics" whose work we have just referred to This is perhaps the greatest eugenic family on record

The Bach family of musicians is another outstanding example of the heredity of genius The best known member of the family is the famous Johann Sebastian Bach In six generations of Bachs there were 47 musicians of note 29 of whom ranked high in musical circles Johann Sebastian Bach was married twice and both times to a relative bearing the name of Bach His father married an aunt. There was a great deal of rather close intermarriage in the family which seems to have helped to concentrate and preserve the high qualities of the stock

Most of the work done on the heredity of mental traits has been expended on the study of defective and abnormal heredity including feeble mindedness and the various so-called insanities

The heredity of Feeble-mindedness—Feeble mindedness as defined by Goddard, is a state of mental defect existing from birth or from an early age and due to incomplete or abnormal development in consequence of which the person affected is incapable of performing his duties as a member of society in the position of life to which he is born This is not a very exact definition for according to the statement, a normal individual born into a community of geniuses might be classed as feeble minded More specific are the following definitions of various types of mental defectives An idiot is one who, when adult, has no greater capacity to learn than a child of two years or less An imbecile is one who rates mentally between two and seven years A moron is one who rates mentally from seven to twelve years Usually the so called feeble minded individual is either an imbecile or a moron and much more often the latter than the former Obviously, then, there are many kinds and degrees of feeble mindedness and it will often be difficult to draw the line between the high grade moron types and the lower levels of normal individuals This classification says East "is arbitrary, but it serves a useful purpose when dealing with feeble mindedness as a social problem Medically and genetically it means nothing—at present If this is true and we believe it at least largely so attempts to deal with feeble mindedness as a simple Mendelian recessive are likely to be only partially successful

We must therefore take all genetic studies of feeble mindedness with a grain of salt

H H Goddard probably the most distinguished of the students of feeble mindedness, has studied many pedigrees and compiled statistics concerning 300 of the best of these Of the cases of feeble mindedness diagnosed as such by him 164 (54 per cent) are considered unquestion ably hereditary 71 (23 per cent) probably hereditary and the rest probably non hereditary Goddard seems to be convinced that feeble mindedness is due to a single recessive gene He cites 42 cases in which heterozygous phenotypically normal mothers (NF) when mated with feeble minded fathers (FF) produced 71 feeble minded and 73 normal offspring out of a total of 144 This is almost too close an approximation to the expected Mendelian ratio of 1 to 1 From 26 matings of apparently heterozygous fathers and mothers (presum ably NF) there were produced 122 known children 83 of whom were normal and 39 feeble minded suggesting the expected Mendelian ratio of 3 to 1 Of 476 children of parents both of whom were feeble minded (FF) only 6 were normal in intelligence and these are suspected of being illegitimate In Figures 86 and 87 are presented two typical pedigrees of feeble minded families studied by Goddard The first of these pedi grees (Fig 86) shows the dire effects resulting from the interbreeding of feeble-minded parents The children are all feeble minded except the considerable number that died in infancy presumably because of neglect and ignorance of the parents The second pedigree (Fig 87) illustrates what approximates a controlled scientific experiment for one woman was married twice once to a normal man and once to a feeble minded man and had several children by each All of the off spring from the normal father are normal (but evidently heterozy gotes) while all those of the feeble minded father were feeble minded and otherwise abnormal

It is interesting to note that a very large proportion of juvenile criminals and prostitutes when given the Binet test rank as feeble minded Tests of juvenile criminals in various states show the fol lowing facts In New Jersey 46 per cent of juvenile criminals are feeble minded in Ohio 70 per cent in Virginia 79 per cent and in Illinois 89 per cent It would seem to be a conservative estimate that fully half of juvenile criminals are feeble minded

It has also been shown that the great majority of prostitutes and girls who have been placed in reformatories for sex delinquency are feeble minded Tests of large numbers of girls in an Illinois reforma

tory show that 97 per cent are feeble minded In Massachusetts a prominent commission reports that of 300 immoral women under detention in that state 57 per cent were feeble minded while the rest rated from nine to twelve years in mental age On the basis of data

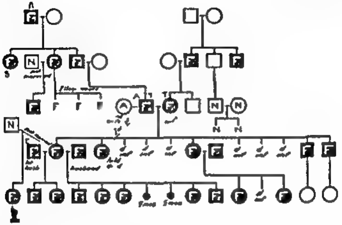


FIG 86 —Pedigree of a family with a high proportion of feeble minded persons (*F*) Squares males circles females *d inf* died in infancy (*From Davenport after Goddard*)

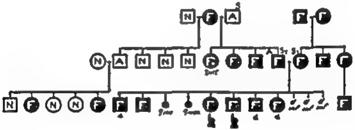


FIG 87 —Pedigree of a family in which the feeble minded grandmother married twice by a normal husband she had normal children but by an alcoholic sex-offending (*Sx*) doubtless feeble minded husband she had only feeble minded children (*From Davenport after Goddard*)

such as these Goddard and others maintain that there is a very intimate relation between crime vice, and feeble mindedness Wipe out the feeble mindedness say they, and you wipe out most of the vice and crime

Feeble mindedness has come to be the most pressing of all eugenic problems—one that should at once be recognized and solved if possible

Statistics seem to indicate that this defect is on the increase certainly it is far too common to be ignored Records show 178 000 mental defectives in Great Britain and Ireland in 1921, and these include only the very positive cases It has been estimated by one expert that in the United States one person in every 294 is feeble minded by another expert, one in every 138 In Indiana it is claimed that over 2 per cent of the population of ten unselected counties are mental defectives If the incidence is the same in the whole state there are 56 000 defectives in Indiana alone and Indiana is in no way exceptional Calculations indicate that in the United States as a whole there are not less than half a million feeble minded individuals and several times that many individuals phenotypically normal but carrying the gene or genes for feeble mindedness A large proportion of these individuals are charges of the various states and cost the public many millions of dollars annually without contributing anything of value to the community

Insanity and heredity —A great deal of careful work has been done on the heredity of insanity For example *David Heron* in Scotland has studied 331 family histories exhibiting insanity There are several distinct and different conditions included under the blanket term insanity ' It is obvious that they could not all be determined by the same gene or genes Heron s data on insanity are summed up in the following table

HERON S DATA ON THE HEREDITY OF INSANITY

Parents	Offspring		
	Insane	Sane	Percentage of Insane
Both sane	314	1179	21
One insane	93	299	24
Both insane	4	4	50

These figures are not at all readily fitted into any simple Mendelian ratio Doubtless the various insanities are not due to single Mendelian units but are complex cases That they are to some extent and in some manner hereditary seems beyond question

Rosanoff and Orr two prominent American psychiatrists seem somewhat more sanguine about fitting the insanities into the Mendelian system Their data are given here in tabular form

ROSANOFF AND ORR (DATA ON INHERITANCE OF INSANITY)

(N=Normal I=Insane)

Parents	Matings	Children		
		Neuropath	Normal	Mendelian Expectancy
Both insane (II)	17	54	10	All insane
Only one insane (NI×II)	93	100	230	1 1
Only one insane (NN×II)	14		45	All insane
Both normal (NI×NI)	62	10	215	1 3
Both normal one heterozygous (NN×NI)	70		77	All sane

Eight have not passed the age of incidence

These data might readily be taken to prove that insanity is a simple Mendelian recessive but a scrutiny of the methods of collecting data make geneticists somewhat skeptical The data says Castle "have the scientific value of gossip consisting of answers made by informants to leading questions designed to bring out any weakness in the pedigree Like inquiries made concerning any individual in the community would show him an unmistakable victim of insanity Three fourths of their persons insane for pedigree purposes would be classed as fully normal if they occurred in families free from insane patients Such classification has little scientific value" This statement may be severe, but it seems justified by the fact that persons who are described as a crank easily excited, nervous temperament very nervous erratic excitable , nervous little things bothered her worried a great deal are classed as insane Doubtless many of us who think we are normal might be classed in some of these categories by our acquaintances

As yet it would be quite unsafe to classify any of the insanities as simple Mendelian unit characters The subject is a very complex and difficult one and genetic results will continue to be unsatisfactory until the psychiatrists are able more accurately to diagnose and classify the 'insanities

Pedigrees of royal families—Members of royal families have been used as data for the study of human heredity Records of these individuals and their traits are preserved in the archives and should furnish good material for genetic study The well known writer Frederick Adams Woods has made an exhaustive study of the pedigrees of European royal families and has published the results of these studies

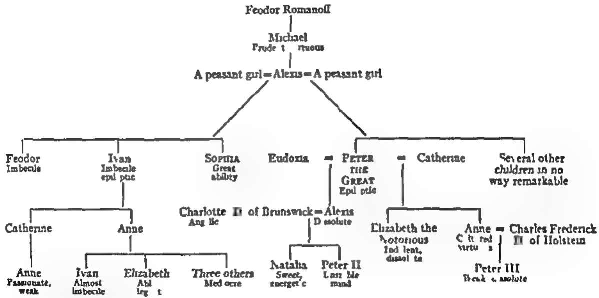
It happens that rather complete data about the members of royal families are to be found in biographical dictionaries From these sources it is usually possible to form a fairly accurate estimate of the capacities of these persons In addition the portraits of most members of royal families are preserved in art galleries The following summary of F A Woods findings is quoted from Pro essor E R Downing

' Early modern European history centers about the doings of a few great men and women Peter the Great of Russia Ferdinand and Isabella and Charles V of Spain Frederick the Great of Prussia Gustavus Adolphus and Charles XII of Sweden are among the most brilliant of these potent individuals that shaped the destinies of Europe during this period It is interesting to note how their characters are determined (and through them national destinies are apparently decided in no small measure) by the hereditary concentration of ability due to lucky royal matings and how their genius is dissipated by unwise matings

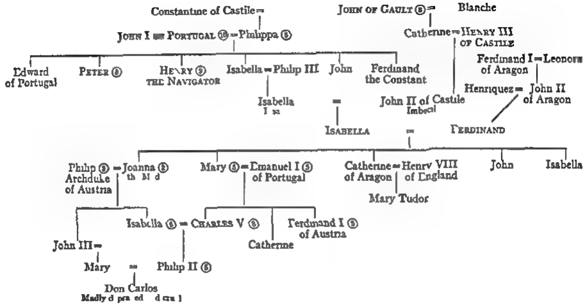
Peter the Great of Russia came as a brilliant type from a good stock though with a very evident taint of epilepsy and feeble mindedness He himself was an epileptic His father grandfather and great grandfather had been men of large ability They had married peasant girls as was the custom of the czars Peter s own brothers and sisters were in no way remarkable His half sister Sophia was a woman of marked ability although two of her brothers were imbeciles one also an epileptic As will be seen from the pedigree the epilepsy imbecility and mediocrity appear in both Peter s children and grand children as well as in those of his imbecile half brother Ivan It is interesting to note from the pedigree that the feeble mindedness and epilepsy seem to cling to the males quite persistently The females of the family are much more apt to be brilliant and virtuous Peter the Great s own son Alexis was a poor dissolute specimen and although he married Charlotte the angelic daughter of a great line the house of Brunswick the son of this mating was Peter II of unstable mind while the daughter Natalia was as sweet as she was energetic

Isabella and Ferdinand were both descendants from lines of very great individuals although in each case there is insanity in the family Isabella herself comes from an insane mother and an imbecile father but her grandparents and great grandparents were well balanced and able The data for the charts of these royal families were taken largely from F A Woods s *Mental and Moral Heredity in Royalty* supplemented with information from other sources He grades the

THE ROMANOFFS OF RUSSIA PETER THE GREAT



FERDINAND AND ISABELLA



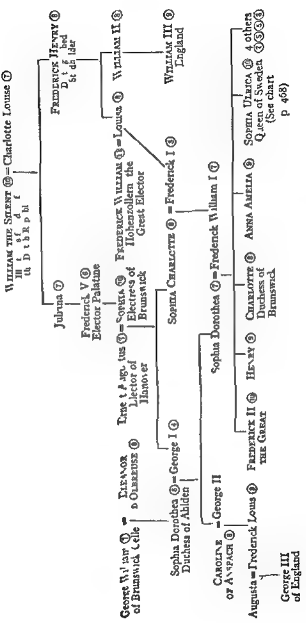
individuals on a scale of 10 Ten represents very high ability as determined by the comparative amount of space and laudation given to the individual in such standard works as Lippincott s *Biographical Dictionary* Five out of eight of Isabella s great grandparents rank very high John the Great of Portugal twice her great grandfather, has a grade of 10 John of Gault twice her great grandfather, has a grade of 8 as does also John of Castile while Henry III of Castile one of her grandparents is designated the model king Ferdinand I of Aragon the grandfather of Ferdinand is a brother of this same Henry III of Castile and is also an exceedingly able king Of the children of Ferdinand and Isabella most were mediocre or distinctly inferior Joanna was insane In the next generation however, appears Charles V whose reign marked the acme of Spain s greatness partially due to his own ability partially due to the momentum of those movements that were instituted by his illustrious grandparents Charles V married his own cousin as did also John III Children of these two matings married and Don Carlos child of this latter marriage, was madly depraved and cruel

"When insanity and brilliancy are found in the ancestry it seems merely a matter of chance as to whether the determiners for greatness will be thrown together in the union of sperm and egg or those for insanity We can predict with some certainty that in a large number of offspring ability will reappear and insanity will reappear but just what individual each will strike it is impossible to prophesy without knowing much more definitely the nature of the germ plasm involved One may say that the convergence of a number of lines of descent from great ancestors toward one individual makes it probable that he will be exceptionally able

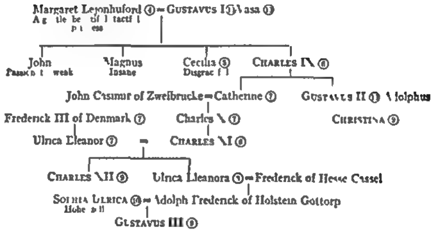
"This is nowhere better illustrated than in the family tree of Frederick the Great of the Prussian house of Hohenzollern as will be seen from the chart on page 467 Of his great grandparents three scale 10, one 9 one 8 two 7, and one 6 Not one is below mediocrity, and the majority are of very high grade Of his fourteen ancestors back three generations only one is distinctly inferior Of his brothers and sisters *four are distinctly great three mediocre* and one inferior

"It is interesting to trace the effect of the mating of such splendid stock with another brilliant line that of the Swedish royal house Gustavus I or Gustavus Vasa is another instance of the brilliant mutant, with some taint of neurosis He married a gentle and tactful princess their son Charles IX was a very able man although of their

THE HOHENZOLLERNS OF PRUSSIA PEDIGREE OF FREDERICK THE GREAT



CHARLES THE GREAT (XII) OF SWEDEN



three other children one was insane and two weak The children of Charles IX were both remarkably able The daughter Catherine becomes the mother of a later succession of kings. Her son Charles X and his son Charles XI were rather mediocre but Charles XI with this fine stock behind him married Ulrica Eleanor (7) granddaughter of Christian IV of Denmark the most brilliant of all Danish sovereigns, and Charles XII their son is pronounced by Voltaire the most remarkable man who ever existed Charles XII had no children the succession passed to his sister s son Adolph Frederick of Holstein Gottorp who married Louisa Ulrica sister of Frederick the Great of Prussia The result of this union of two great lines of hereditary ability was Gustavus III a fit successor of Gustavus Vasa Gustavus Adolphus and Charles XII he was a prodigy of talents statesman poet dramatist.'

CHAPTER XXXVI

THE STATISTICAL STUDY OF HEREDITY IN MAN

Introduction —A good example of this method is afforded by Popenoe and Johnson s studies of the heredity of longevity (chap xxxix) Other examples are found in Heron s and in Orr and Rosenoff s studies of the heredity of insanity presented in the last chapter The proof of a given character being hereditary is believed to be attained when it is shown that affected parents have a significantly larger proportion of affected offspring than have non affected parents

The statement that twinning is hereditary is based on the fact that twins are far more common in certain strains than in the general population A twin birth occurs in about 1 out of every 88 confinements C H Danforth found that in the case of 50 new born twins there were 171 single brothers and sisters and 10 pairs of twin brothers and sisters a ratio of about 1 to 18 as compared with that in the general population, 1 to 88 Moreover, with respect to the mothers of these twins, their brothers and sisters numbered 318 singles to 10 pairs of twins, a ratio of 1 to 32 With respect to the fathers of these twins there were 219 brothers and sisters born singly and 8 pairs of twin brothers and sisters a ratio of 1 to 37 A number of similar studies give comparable results showing that twinning has a hereditary basis, but indicating nothing as to the exact mode of heredity

The strength of heredity between different groups of relatives has been determined for a large number of human characters by determining the coefficient of correlation (see chap xliii) existing between selected groups Complete correlation is represented by the unit 1 If correlation is 1 heredity is perfect and various grades of imperfect heredity are represented by decimals such as 0 9 0 6, 0 25 etc It has been shown that for most characters the correlation of offspring to fathers is about 0 4 the same to mothers The correlation between sibs (brothers and sisters) is about 0 5 that between cousins about 0 25, that between one egg (identical) twins 0 9+ These indices of correlation run strictly parallel with degrees of closeness of genetic relationship

GALTON'S STATISTICAL STUDIES OF HEREDITY IN MAN

Galton was the first to make extensive use of the statistical method of studying the degree of heredity existing between parents and offspring and between sibs

His first investigation concerned itself with the heredity of stature a highly variable character in man He tried to find just how nearly parents and offspring are correlated as to adult stature Certain difficulties were met at the outset First there is a pronounced sexual dimorphism in stature males being considerably taller on the average than females To get rid of this difficulty he first determined that males are on the average about 1 inch to the foot taller than females and then transmuted all female statures into equivalent male statures by adding an inch to the foot to the stature of each female Second there are always two parents and they may be of very different statures even after the mother's stature is transmuted into the male equivalent To overcome this difficulty he averaged the statures of each pair of parents and called it the mid parent stature The statures of the mid parents were grouped into nine classes ranging from 64 to 73 inches each class having a range of an inch Thus one class consisted of those mid parents falling between 72 and 73 inches the next class from 71 to 72 inches and so on down to the shortest class from 64 to 65 inches The following schematic diagram (Fig 88) shows the extent to which offspring inherit stature differences from the parents If heredity were perfect parent and offspring statures would coincide on the diagonal line but they do not coincide Average parents have nearly average offspring but very tall and very short parents have offspring decidedly less tall or less short respectively than their parents In the chart the arrow heads indicate the points where the average statures of offspring of each of the mid parent classes fall Note that mid parents which average a little over 64 inches have offspring averaging about $65\frac{1}{2}$ inches and that mid parents which have an average stature of $71\frac{1}{2}$ inches have offspring averaging 70 inches It is clear that on the average the more exceptional the mid parents are the more the offspring regress toward the mean stature of the group or toward mediocrity This is true of all but the extreme tall group where there is only a half inch of regression in the offspring The reason for this is probably associated with the fact that very tall persons are homozygous (double recessives) shortness of stature being incompletely dominant over tallness

Galton calculated that with regard to stature the offspring of

exceptional parents tend to be on the average one third less exceptional than the parents This he called the *Law of Filial Regression*

Similar results were obtained with several other types of human differences that were capable of being graded quantitatively and arranged in classes Thus when eye colors were graded on the basis

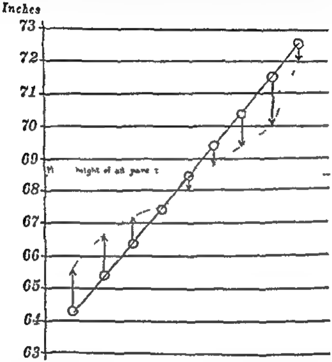


FIG 88 —Diagram to illustrate Galton's Law of Filial Regression as shown in the stature of parents and children The mean height of all parents is shown by the dotted line between 68 and 69 inches The circles through which the diagonal line runs represent the heights of graded groups of parents and the arrow heads indicate the average heights of their children The offspring of undersized parents are taller and of oversized parents are shorter than their respective parents (*From Conklin after Walter*)

of the amount of pigment in the iris and arranged in nine or ten classes it was found that there was practically the same amount of filial regression as there was in the case of stature This was true for all except the pure blue eyed parents with no pigment in the front of the iris where no regression in the offspring was noted Blue eyed individuals are of course homozygous if they are really blue-eyed in the genetic sense

The same law was shown to hold also for mental characters or grades of mental ability "The more bountifully a parent is gifted by nature, says Galton the more rare will be his good fortune if he begets a son as richly endowed as himself Galton considered that any law that applied to such diverse characters as stature eye color and mental ability must be a universal law of heredity

The problem then arose as to the reason why heredity between parents and offspring is so imperfect Let us remember that Galton did all his work long before the rediscovery of Mendel s publications Had he known about Mendel s laws about the difference between

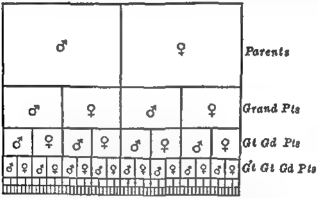


FIG 89 —Diagram to illustrate Galton s Law of Ancestral Shares in Inheritance The whole heritage is represented by the entire rectangle that derived from each progenitor by the smaller squares the number of the latter doubles in each ascending generation while its area is halved. (*From Conklin after Thomson*)

phenotypic and genotypic conditions and that recessive characters concealed for some generations crop out when two recessive genes meet he would have understood at once why offspring are not always as exceptional as parents Without any of this background Galton had to solve the problem of imperfect heredity in his own way

He arrived at a conclusion not unlike that of Weismann that inheritance does not come from the bodies of parents but from a racial 'stirp which is about the same as Weismann s germ plasm The reason assigned for filial regression was that offspring do not get all their hereditary characters from their immediate parents but some of it comes from the four grandparents some from the eight great grand parents and some from more remote ancestors Just how much each of the different grades of ancestors contribute to the total heritage of

Progesterone can maintain life in adrenalectomized animals [11] The luteal phase is associated with large amounts of glycogen in the endometrium Progesterone is considered an antiestrogen and the reduction in alkaline phosphatase activity during the secretory phase may be concerned with glycogen metabolism [17]

(3) At birth the ill prepared immature fetus must suddenly transfer to an aerobic existence Glycogen is preferred to glucose for aerobic metabolism A low level of anaerobic metabolism prevails as long as an excess of glycogen is available [18] The fetal rat has been shown to be a glycogen *storing and glycogen consuming engine* [19] *Being* a polysaccharide reservoir the fetus requires large additional amounts of stored water This may be the safeguard against excessive dehydration

(4) Immature fetuses have a minimal amount of fat and must use glycogen for energy The 11 and 11 17 oxysteroids regulate carbohydrate metabolism by increasing the peripheral utilization of fat while decreasing the utilization of carbohydrate [20] Progesterone is related to desoxycorticosterone which is somewhat antagonistic to the 11 and 11 17 oxysteroids and it may have a similar inhibiting effect on the utilization of fats

(5) The fetus is a mobile organism using muscle glycogen and converting it to lactic acid This lactic acid is changed to liver glycogen by the placenta which has the power to remove both maternal and fetal lactic acid from the circulation for this purpose This pattern demonstrated in animals [21,22] may also be present in man

(6) In summary to convert to an aerobic metabolism the immature fetus needs large amounts of glycogen not ordinarily available Progesterone may have a role in glyconeogenesis and glycogen storage It does inhibit *uterine activity particularly at the placental site* The placenta is capable of converting lactic acid derived from muscle glycogen to liver glycogen for energy purposes Thus progesterone may enhance this activity as well as inhibit the consumption of the practically nonexistent fetal fat The glycogen developed through this process will hold large amounts of water possibly preventing or allaying to some degree the dangers of dehydration Progesterone may be the key to this entire process 17 HPC is a progestational drug and in the above mechanisms may act exactly as does progesterone

Summary and Conclusions

Fifty nine pregnant women treated with 17 HPC are presented in 3 groups the first of which includes 40 with spontaneous premature rupture of the membranes The remainder had painful uterine contractions or distension associated with several different causes Neither premature nor term labor was prevented although many of the patients with painful contractions and uterine disease obtained rapid and relatively complete relief on adequate dosage individualized for each patient Fetal salvage in the 1000 to 2000 gm group was significantly improved ($p = 0.03$) in those treated with 17 HPC A theoretical explanation for this improvement is attempted

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TREATMENT OF HUMAN DIABETIC PREGNANCIES WITH ESTRADIOL VALERATE AND 17α HYDROXYPROGESTERONE 17 n CAPROATE

By Luke Gillespie, Lloyd I. Sexton and Priscilla White
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The Joslin Clinic has cared for more than eleven hundred viable diabetic pregnancies. As a result of this experience we of the Joslin Clinic believe that the use of female sex hormones is an essential and valuable part of the treatment of such pregnancies, especially in patients who have been diabetic for a long time and in patients who have definite vascular, retinal and/or renal disease.

We believe the following changes are associated with female sex hormone therapy of pregnant diabetics:

(1) Decreased incidence of spontaneous abortion and premature labor. Our previable failure rate averages 10 per cent. This compares favorably with the rate of any obstetrical clinic.

(2) Decrease in the degree but not in incidence of hydramnios. One result of a decrease in the degree of hydramnios is that fewer patients have premature rupture of the membranes and premature labor.

(3) Decrease in the incidence of true toxemia of pregnancy. In our diabetic patients this incidence amounted to 2 per cent.

(4) Decrease in the number of intrauterine deaths.

(5) Higher fetal survival rate.

(6) Changes in the placenta. *The placentas in the diabetic pregnant* patients treated with female sex hormones closely resemble those of the nondiabetic pregnant women and cannot be recognized either grossly or microscopically by the pathologist as being the placentas of diabetic mothers.

(7) *Changes in the infant. Most of our infants no longer have the so* called Cushingoid appearance once described as typical of the infant of a diabetic and many cannot be recognized by the pediatricians in the nursery as being the infants of diabetic mothers.

(8) Decrease in the weight of infants. For comparable gestational ages our infants now average one pound less than in patients who did not receive female sex hormone therapy.

(9) Less progression in vascular disease in mothers. Only 2 or 3 per cent of our mothers show a definite progression of vascular disease, particularly in the retina, after the pregnancy is terminated.

(10) Possible improvement in maternal diabetes postpartum for months and possibly years. Many of our patients have shown definite clinical improvement in their diabetes as judged by the amount of insulin required and many of them have shown marked redirection of their insulin projection curve. Two things cannot be changed by the use of female sex hormones

TABLE 1

CLASSIFICATION OF PREGNANT DIABETICS

Class A	Glucose tolerance test diabetics—noninsulin users
Class B	Age at onset of diabetes mellitus—over 20 years Duration of diabetes mellitus—under 10 years No vascular disease
Class C	Age at onset of diabetes mellitus—10 to 19 years Duration of diabetes mellitus—10 to 19 years No vascular disease
Class D	Age at onset of diabetes mellitus—under 10 years Duration of diabetes mellitus—over 20 years Retinitis Calcification of leg vessels
Class F	Patients with calcification of pelvic vessels
Class F	Patients with nephritis

the occurrence of congenital anomalies in the infants and hyperplasia of the islets of Langerhans in the infants who do not survive.

Since 1936 979 studied pregnancies have reached viability. By studied we mean patients whose blood and urine have been assayed for female sex hormone level. Of this group 819 patients received female sex hormone therapy. Fetal survival rate in this group was 87 per cent. One hundred and sixty patients did not receive female sex hormone therapy. Fetal survival in this group was 65 per cent. The female sex hormones used stilbestrol and progesterone were given by daily intramuscular injection.

Priscilla White's classification of pregnant diabetics and the dosage *schedule of female sex hormones formerly used are shown in TABLES 1 and 2.*

Stilbestrol and progesterone were given by daily intramuscular injection. Husbands, mothers, friends and neighbors were taught to give these injections. Complications were a few cases of local allergy and one or two abscesses a year. Toward the end of pregnancy large volumes of material *were being given daily and at times there was hardly any area available for* further injection.

Prolonged postpartum bleeding was not a real problem. One or two patients a year would require curettage of the uterus to stop such bleeding.

No cases of uterine or ovarian malignancy can be traced to the use of these *hormones even in such large doses.*

TABLE 2

SCHEDULE OF HORMONE TREATMENT ACCORDING TO CLASSIFICATION

Intramuscular Injection of Both Stilbestrol and Progesterone—Milligrams of Each

Week of pregnancy	Class B	Class C	Class D	Class E	Class F
0–16	25	25	25	25	25
17–19	25	25	50	50	50
20–23	50	50	100	100	100
24–29	100	100	125	175	125
30–33	100	100	150	150	150
34–37	125	125	200	200–250	200–250

Present Series

During the past year fifty human diabetic pregnancies have been treated with weekly injections of estradiol valerate (Delestrogen) and 17α hydroxy progesterone 17 *n* caproate (Delalutin). The pregnancy classifications of these patients is shown in TABLE 3.

TABLE 3
FIFTY PATIENTS DELESTROGEN AND DELALUTIN

Class A	0
Class B	9
Class C	18 } Eighty two per cent severe diabetics
Class D	19 }
Class E	0 }
Class F	4 }
Patients with retinitis	13
Patients with retinitis proliferans	3
Patients with nephritis	4

Dosage schedule: As soon as a definite diagnosis of pregnancy was established by either clinical or biological tests hormone therapy was started with Delestrogen (1 cc) and Delalutin (1 cc) intramuscularly weekly. This dose was gradually increased to 10 cc of each increasing to 12.5 and occasionally to 15 cc in very poor risk patients. The total amount of Delestrogen and Delalutin received weekly corresponds roughly to the weekly amounts of stilbestrol and progesterone our patients had received previously. The results of fifty pregnancies are shown in TABLES 4 and 5, the week of delivery in TABLE 6, and the type of delivery in TABLE 7.

Failures. There were 7 failures, 4 intrauterine deaths and 3 neonatal

TABLE 4
FIFTY PATIENTS DELESTROGEN AND DELALUTIN
Viability—all Patients Completed at Least 28 Weeks of Pregnancy

Intrauterine deaths	4
Live born infants	46
Neonatal deaths	3
Infant survivals	43-86%
Congenital anomalies	5-10%

TABLE 5
FIFTY PATIENTS DELESTROGEN AND DELALUTIN

Thirteen patients with retinitis—10 infant survivals
Three patients with retinitis proliferans—2 infant survivals
Four patients with nephritis—3 infant survivals

TABLE 6
FIFTY PATIENTS DELESTROGEN AND DELALUTIN

Week of delivery	30th— 2
	32nd— 1
	33rd— 1
	34th— 4
	35th—16
	36th—24
	37th— 2

TABLE 7

FIFTY PATIENTS DELESTROGEN AND DELALUTIN

Type of delivery	
Pelvic	24
Primipara	7
Multipara	14
Caesarean section	26
Primipara	11—6 failed inductions
Repeat sections	15

deaths The intrauterine deaths were as follows (1) microcephalic infant (2) patient with a bicornuate completely septate uterus (intrauterine death at 29 weeks) (3) uncooperative patient with poor diabetic control (intrauterine death at 34 weeks) and (4) intrauterine death at 34 weeks (when the infant was delivered the cord was wound tightly around the neck) the 3 neonatal deaths were as follows (1) premature rupture of membranes and premature labor at 30 weeks (patient a diabetic dwarf) (2) separation of the placenta at 30 weeks and (3) separation of placenta at 35 weeks (patient a diabetic dwarf)

Outstanding successes These included (1) one patient with 5 previous pregnancy failures (2) one patient with a classification of F and with albuminuria of 1000 mg per day whose nonprotein nitrogen was 60 one patient with a classification of F and previous interruption of pregnancy for extensive retinitis (4) one patient with a classification of F albuminuria hypertension calcification of ankle and pelvic vessels retinal hemorrhages and exudation and retinitis proliferans and (5) one patient with thyrotoxicosis who underwent a thyroidectomy in early pregnancy

There were 16 patients with retinitis Thirteen patients had retinal arteriosclerosis or hemorrhage or exudate Ten of these 13 produced good infants Three patients had retinitis proliferans 2 of these 3 had good infants

Patient acceptance No difficulty was encountered in recommending weekly hormone injections to these patients Many of them in earlier pregnancies had received daily intramuscular injections this new schedule with fewer injections and much smaller volume of injected material seemed to them a tremendous improvement

Complications Complications of Delestrogen and Delalutin therapy have included (1) no local inflammation or abscess formation (2) 2 local allergies (... ing rash and the like) (3) 1 generalized allergic reaction (mild angio ... tic edema) (4) no pelvic pain (5) no nausea vomiting or generalized malaise (6) 5 moderate and 1 severe hydramnios (7) 2 separations of the placenta (8) 1 premature rupture of membranes (9) breast engorgement and lactation (in contrast to absence of both breast engorgement and lactation with daily intramuscular stilbestrol and progesterone almost all of these patients had some degree of breast engorgement and 6 lactated to some degree for a short time) and (10) prolonged postpartum bleeding (1 patient with uterine atony on the day of delivery required a curettage 4 patients have had prolonged bleeding at home 2 responding to rest and ergotrate and 2 returning to the hospital for curettage of the uterus)

Hormone assays Blood chorionic gonadotropin levels have been within our normal limits in 95 per cent of the analyses performed No urinary pregnanetriol assays have been done Only 10 (20 per cent) of the patients had what we consider average urinary pregnanediol excretion assays for diabetic pregnancy treated with female sex hormone therapy All the others had curves lower than average

Clinical Impressions

We realize that this is a small number of patients and we realize that it is impossible to be completely impartial and objective in observing newer methods of treatment Nevertheless, we believe that this particular group of patients which included many severe diabetics has gone through pregnancy more smoothly and uneventfully than any group we have ever handled Those patients who succeeded did so with fewer diabetic and obstetrical complications than we usually encounter This same feeling has been expressed by the pediatricians who care for these infants Of these patients a larger number of infants were transferred from the premature nursery to the regular nursery and left the hospital with their mothers than is usual with these patients

Summary and Conclusion

Fifty human diabetic pregnancies were treated with weekly intramuscular injections of Delestrogen and Delalutin Injections were started as soon as a definite diagnosis of pregnancy could be made and were continued up to within a few days of delivery The initial dose of each drug was 1 cc increasing gradually to 10 cc of each Eighty two per cent of these patients were severe diabetics Sixteen of these had retinitis and 4 had nephritis

All of these pregnancies reached viability The fetal survival rate was 86 per cent

Statistically these results are as good as any we have ever achieved Actually they are better for this was a poor risk group with many severe diabetics Complications of hormone therapy were minimal There were a few mild local allergic reactions of short duration One patient developed mild angioneurotic edema Two patients were forced to return to the hospital for curettage of the uterus for prolonged postpartum bleeding

The blood chorionic gonadotropin assays were normal in 95 per cent of the patients No urinary pregnanetriol excretion assays were done Urinary pregnanediol excretion assays were done on almost every patient Only 10 per cent of the patients had a normal curve of diabetic pregnancy All others had pregnanediol curves lower than the curve we consider the average for diabetic pregnancies

Acknowledgments

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Discussion of the Paper

GEORGE P HECKEL (*Rochester N Y*) One question that always puzzles me is how you can separate the effect of improved treatment of diabetes from the effect of hormone treatment

LUKE GILLESPIE (*Harvard Medical School Boston Mass*) Those 160 patients who did not receive hormone treatment extend back over a certain number of years We realize that some improvements are due to the improvements in obstetrical and diabetic treatment better anesthesia perhaps better surgery and better premature nursing We realize that all of the improvement is not due solely to the use of female sex hormone therapy That is only one of seven major points of treatment

We always have a few patients who do not receive female sex hormone therapy Some live at a distance Some are correspondence cases Occasionally we are trying to get a few controls of our own If a patient refuses to accept hormones we can be certain that she is not going to carry out the rest of our prescribed care and treatment thus it is unfair to say that she fails simply because she did not receive the hormone However even in the few patients willingly selected as controls we find sooner or later before the pregnancy is over that for one reason or another we are starting hormone therapy

We know this is quite in contrast to the practice of some of the diabetic clinics For instance Pederson maintains that he gets just as good results with special care of diabetes We have never been able to obtain as good results in cases without female sex hormones as we have with although we will agree that not all of the improvement of fetal survival is due to hormones Of course we cannot use hormones and neglect any part of the obstetrical care the diabetic care or particularly the care of the newborn infant In other words we cannot simply administer one injection a week and then turn the patient loose and assume that she is going to do very well

I agree with you in that the evaluation is difficult You notice that I have said that these things were *associated* with female sex hormone therapy We have not said they were directly dependent upon it but our best results do seem to occur in those patients who are treated with the hormones

SUMMARY

By Abraham E. Rakoff
Jefferson Medical College Philadelphia Pa

Dresses kept long enough are bound to come back in style that seems to be the case with progesterone The great enthusiasm in the thirties for progesterone studies has now returned as evidenced by the work reported in this monograph Progesterone itself has been reviewed in these pages and even a few of its previously well accepted actions have come up for some discussion or challenge Ethisterone or anhydrohydroxyprogesterone has been discussed in many of these studies as a standard of comparison for the new oral progestational agents 17α Hydroxyprogesterone caproate and other esters of 17α hydroxyprogesterone particularly the acetate or acetoxyprogesterone have been discussed Considerable attention has been given 19 norethisterone which I shall refer to as Norlutin and also the methyl and vinyl analogues of this compound Norethynodrel an estrenone compound which together with an added 1 5 per cent of ethynyl estradiol 3 methyl ether has been referred to as Enovid has been discussed as have other 17 alkyl derivatives of this compound Mention has also been made of the 9 and 12 halo 11 oxygenated progesterones as new oral progestational hormones

In the first part of the monograph considerable attention is devoted to the actions of these new progestational hormones on animals and it becomes obvious that we are dealing with a group of hormones in which there is a great diversity of biological action Indeed there has been considerable controversy as to what constitutes a progestational hormone Even though Greenblatt has given us a new criterion I do not think any single definition has been advanced that would be acceptable to all the contributors to this publication In other words it is obvious that we have a number of agents with diversified actions that provide good investigative material for both the laboratory and the clinical worker Once familiar with the various actions of these individual compounds we shall have available a selection of different progesteronelike hormones for different particular clinical and laboratory purposes

The chemistry and biological action of Delalutin in animals are reviewed by Kessler Borman and Fried It is shown in these as well as other papers that this compound exerts in animals a typical progesteronic effect on the *endometrium but a much more prolonged duration of action* It is also shown that Delalutin has essentially no estrogenic activity and that it is not androgenic As far as any possible anabolic effects are concerned there is obviously some species difference For many species no anabolic effect has been noted but on the other hand Gassner and Reifenstein give very striking evidence of the anabolic effects of this agent when given together with long acting estrogens and androgens in accelerating the weight gain in cattle and in upgrading the beef

In comparative studies by Zarrow and his associates using different end

points in an effort to evaluate the effects of various progestational agents we see that Delalutin is extremely active by the Hooker Forbes test and that it had some activity in the chick oviduct and rabbit test but not in the deciduoma maintaining test in rats and mice whereas progesterone itself was active

Velardo shows that Delalutin given to mice prior to conception did not have a deleterious effect on the endometrium and the litter size of rats whereas progesterone had a markedly deleterious effect He suggested that this difference in litter size is due to differences in the metabolites in the two compounds

Smithberg shows that Delalutin given to prepuberal female mice stimulated with gonadotropin to ovulate and mate would foster implantation but that it is not capable of maintaining pregnancy In the discussion following Velardo suggested that perhaps estrogen may be necessary

It has been interesting to note also that Johnson had great success in increasing the breeding efficiency of infertile cattle by the addition or administration of Delalutin Nalbandov also showed that the embryonal survival was significantly reduced in pigs and probably in sheep but not in rats by progesterone therapy following conception

Regarding the biological action of the 19 nor steroids on animals we might first consider the excellent paper by McGinty and Djerassi on the chemical investigations that led to the synthesis of the 19 nor steroids These data show that Norlutin is as active orally as by intramuscular injection and that it has a progestational potency about five times that of ethynyltestosterone It has slight oral estrogenic activity negligible androgenic and slight anabolic actions

Of the analogues mentioned of the 19 nor derivatives androgenicity appeared to increase in the following order the vinyl derivative the ethyl derivative and then the methyl derivative which appears to be as androgenic as methyl testosterone itself

Norlutin appears to have antigonadotropic activity in animals Zarrow s tests showed that it is active in the progestational reaction the decidual reaction and in the chick oviduct test

The biological actions of Enovid quite comparable to those of Norlutin have been excellently reviewed by Saunders and Drill Enovid has an oral progestational activity of a magnitude comparable to that by parenteral [illegible]ection It has some estrogenic activity There has been controversy as [illegible]hether this is due entirely to a contaminating estrogen or is also attribut[illegible] to some endogenous estrogenic action of the compound itself At any rate reasons are given as to why this compound is purposely fortified with estrogen primarily to prevent bleeding during administration and to enhance certain desirable factors Enovid was also antigonadotropic but it did not block exogenous gonadotropin

The 19 nor steroids apparently block ovulation and in this action appear to be more effective than progesterone Enovid is not androgenic It would appear to have slight anabolic action It does not maintain pregnancy in the ovariectomized animal

For convenience the studies of the effects of these compounds on man might be divided into several headings First are the papers that deal with the action on the endometrium (those by Boschann Epstein, Kupperman and Cutler Wied and Davis Shah Long and Southam Whitelaw and Roland) In this section I think that certain common denominators regarding the action of these hormones become apparent It was evident that Delalutin could produce a good secretory endometrium in the estrogen primed individual It was also noted that if the long acting progesterone and long acting estrogen are continued over a prolonged period a decidual reaction is produced These compounds will favor the deposition of glycogen in the endometrium

Concerning the 19 nor compounds their action upon the endometrium was obviously atypical It might be fair to say that most workers agree that these compounds at first hasten a progesteronic action so that in a few days one obtains a picture comparable perhaps to an 18 or 19 day endometrium except in that continued administration seems either to arrest the development of the glands at that point or perhaps exhaust their secretory activity and that thereafter the continued action would be mostly on the stromal cells

Long and her associates have presented some beautiful microphotographs of the deposition of glycogen in the stromal cells They have also shown that lipids increase under the influence of these compounds and that the alkaline phosphatase is distributed in a pattern comparable to that seen in the proliferative rather than in the secretory phase

There are also many microphotographs of the atypical pictures that would be produced if the 19 nor compounds were continued for any length of time Here we find marked stromal hyperplasias with relatively inactive or atrophic glandular patterns We find also from Greenblatt and his associates that bleeding can be deferred with some of the 19 nor compounds for a prolonged period of time as it can with the long acting estrogen and progesterone but that with the 19 nor compounds this bleeding can be held off even if treatment is started the seventh day after ovulation Greenblatt suggests that this constitutes a test for true progesterone activity

As far as the effects of these compounds on human vaginal smears are concerned in the main these compounds produce regressive changes The change seen with Delalutin is typical of the normal corpus luteum phase With the 19 nor compounds the vaginal smear picture particularly shown by Wied and Davis may be atypical because of the presence of estrogen Consequently the shift to a corpus luteum pattern on the vaginal smear does not occur promptly or typically

These compounds all produced a hyperthermic reaction The hyperthermic reaction of the 19 nor compounds commented upon by a number of workers was particularly striking and appeared in some instances, to be out of proportion to the effect upon the endometrium suggesting that perhaps further investigation of this action is indicated

Apparently little is known concerning the intermediary metabolism of these compounds Everyone agrees that neither Delalutin nor the 19 nor compounds were excreted as sodium pregnanediol a fact that has some advan

tages and disadvantages for clinical studies The disadvantage is that we cannot measure the metabolic excretion product the advantage is that it does not therefore interfere with measurements of the patient s own corpus luteum activity while on treatment

The effect of these compounds on ovulation in man has been mentioned by a number of workers The 19 nor compounds particularly if started early in the cycle inhibit ovulation and consequently have been used for con traceptive purposes Whether they will continue to inhibit ovulation in sub sequent cycles on the same do age is I believe a question still not settled Some of the data particularly those presented by Pincus Rock and Garcia indicate that this was the case Their observations also indicated prompt return of ovulation after cessation of treatment Several investigators have raised the point that possible harmful endocrine or metabolic effects may result from long term use of these compounds

The 19 nor compounds Enovid and Norlutin both inhibit gonadotropin in the animal and in man The paper by Epstein Kupperman and Cutler actually reports a depression of gonadotropin in the menopausal female and the azoospermic male Whether it is influenced by the estrogenic component is open to question It would appear that usually Delalutin does not inhibit the follicle stimulating hormone although one exception was reported by Clark and Greenblatt

Regarding the other metabolic effects in man the paper by Landau and his associates is particularly interesting These investigators point out that progesterone itself is catabolic From their studies it would appear that progesterone under the conditions in which it was used was salt dissipating a contradiction of older studies indicating that it causes salt and water retention Delalutin was catabolic but had no effect on sodium excretion in most of the instances quoted The 19 nor compounds were anabolic and sometimes salt retaining or had not effect on sodium and chloride There is therefore a distinct difference between the effects of these compounds

The effects of these hormones on the testes were evaluated in the paper by Heller Laidlaw Harvey and Nelson The compounds were given to a number of convict volunteers with sperm counts biopsies and hormone assays before during and following therapy It is shown conclusively that these compounds will cause a rather rapid suppression of testicular function and that they will cause a fall in the sperm count to zero with coincident icular damage but with recovery at a later time sometimes 24 weeks r with possibly a rebound to a level higher than the original There ome que tion as to whether this effect was due to inhibition of gonado tropins That point remains unsettled

Many excellent papers on the effect of these compounds in gynecologic problems are presented These include studies on patients with such men strual dysfunctions as amenorrhea oligomenorrhea and inadequate corpus luteum phase patients with dysfunctional uterine bleeding also patients with anovulatory infertility Data carefully accumulated by Boschann on the effect of Delalutin on the endometrium of women with menstrual dysfunction are presented Southam reviews her results and in a very con

servative fashion, points out that bleeding could be induced with all of these agents with certain treatment patterns and with certain expected results She questions however whether these compounds would do more than that in the amenorrheic patient in other words would induction of bleeding favor the subsequent return of the normal cycle? I do not think her data sufficient to settle this particular point or that they were intended to do so Indeed many of the contributors have discussed amenorrhea in patients in whom the cau e of the amenorrhea was not known or not given Until more can be said concerning the history of the patients being considered perhaps it would be difficult to evaluate the effect of the various compounds on obtaining sub sequent return to normal cycling or subsequent pregnancy in infertile women

Concerning the effect of these compounds on dysfunctional uterine bleed ing treatment plans are described whereby both Delalutin and the 19 nor compounds could be used effectively to stop a bout of bleeding and to obtain subsequent so called medical curettage It would appear from the data pre sented that more rapid hemostasis is usually possible with the 19 nor com pounds than with Delalutin and that subsequent bleeding can be delayed longer with the 19 nor compounds

The problem of infertility was discussed by Tyler and Olson and was also discussed following the paper by Gold and Cohen I think these workers indicated the great difficulty in evaluating the results of anovulatory fertility treated with any one agent They pointed out that when we have an infer tility *problem* we are treating a patient and *not a single factor* and we are treating a patient with many different modalities They show however, certain plans of hormonal treatment that might be used with anovulatory infertility patients I have the impression that both workers seem to prefer the use of these compounds in the last half of the cycle although they might also be used in some instances for subsequent rebound effect in the early part of the cycle Certainly more must be done before we know which of these two plans of treatment will give the better results

Goldzieher brought to our attention the fact that another derivative of 17 hydroxyprogesterone namely the acetate has oral activity whereas the caproate does not He was impressed with its actions on the endometrium in reproducing that of progesterone It would seem however that a higher dosage is necessary than with the other oral compounds Greenblatt found that this compound did not delay menstruation when given late in the normal cycle

Finally we have the rather optimistic reports by the obstetricians on the treatment of threatened abortion the habitually aborting patient the patient with premature labor and the patient whose pregnancy is compli cated by diabetes I am impressed with the very careful data obtained in this connection and by the attempts made at sound evaluation

On the other hand I believe the warning expressed by Goldzieher is not taken amiss namely that proper statistical evaluation of the problem of habitual abortion is extremely difficult What constitutes a good control has never been settled to the satisfaction of all Perhaps until we find an investigator who has enough patients and treats them all the same way

with every other patient receiving no hormonal therapy we may not know the answer because it would seem that even such things as personality and other psychogenic factors may also enter into the problem Until we do know the answer it would seem that these new compounds are of potential value in the field of obstetrics in that they promise to ensure the survival of a greater number of fetuses